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The Effect of Environment on the Genetic Behavior of Irish Potato Progenies.

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THE EFFECT OF ENVIRONMENT ON THE GENETIC BEHAVIOR OF IRISH POTATO PROGENIES

A Dissertation

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Doctor of Philosophy

in

The Department of Horticulture

by
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R.H.J.

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ABSTRACT

The development of potato varieties with improved horticultural characteristics and wider adaptability is important to all segments of the potato industry. Wider adaptability for such important characters as specific gravity, a measure of culinary quality, would be especially important to the consumer of fresh and processed potatoes.

Knowledge of the heritability of characters should be useful in increasing the efficiency of selecting for wider adapted varieties. Research has shown that it is possible to obtain combinations of genes in a variety that will have high specific gravity and other improved characters when grown under one set of environmental conditions, but when grown under another set of conditions the forces of environment often interfere to produce a variety that is not necessarily indicative of its genotype. Certain varieties of potatoes have been observed to show wider adaptability when grown under the wide range of environmental conditions found in the United States.

This study was undertaken to study the effect of environment on the genetic behavior of six characters and to determine if varieties could be developed that would express relatively uniform character expression when grown in the North and South. Special emphasis was placed on specific gravity with concurrent studies made on plant maturity, vigor, tuber shape, tuber eye depth, and tuber appearance.

Ten progeny lines representing several hundred clones were grown in Louisiana and North Dakota. Progeny lines representing first clonal generations were grown in the North. Progeny lines representing second

clonal generations were grown in the North and South. Parents used to develop progeny lines represented wide differences in character expression.

Specific gravity was determined by the potato hydrometer method, weight in water and air, and by the salt brine method. Other determinations were made by an arbitrary rating scale designed specifically for each character.

Specific gravity of tubers from progenies of the second clonal generations were found to be high in the North and low in the South. Tubers from progenies of the first clonal generations grown in the North were intermediate in specific gravity.

The segregation in progenies from all varieties used as parents showed they were highly heterozygous for all characters. Crosses between low x medium and low x high specific gravity parents produced the highest degree of segregation. High specific gravity parents produced progeny with the highest mean specific gravity.

Correlation coefficients computed for various characters from progenies grown in the North and South showed some degree of linear relationship. The highest association was found for tuber shape, followed by plant maturity, vigor, tuber eye depth, specific gravity, and tuber appearance.

The results from the analysis of the data for each of the characters studied showed that there were highly significant differences among the progeny lines. The magnitude of heritability estimates was affected by the parents used to develop the progeny lines. The highest heritability estimates and expected selection advance for specific gravity was found for progenies developed from high specific gravity parents. Heritability estimates for other characters showed variable parental effect for each character and for each progeny line.

Based on this study, it appears that although the forces of environment affected the genetic behavior of all characters, selection could be made quite efficiently for tuber shape, plant maturity, vigor, and tuber eye depth.

This study also showed that if high specific gravity parents are used, a fair degree of success can be achieved in developing varieties that show less environmental effect for specific gravity. Tuber appearance seemed to be the character most affected by environment.

INTRODUCTION

The development of better varieties of potatoes with high specific gravity for processing and fresh use is the ultimate goal of today's potato breeder. The recent trend towards the consumption of processed potatoes has required that new varieties must meet the demand of the processor as well as for fresh use. Essentially, new varieties developed for processed and fresh use should have about the same characteristics. Some important characters should include high yield, smooth tuber shape, shallow depth of eye, and high specific gravity.

For both processed and fresh use, high specific gravity becomes especially important. Research has shown that the yield of processed products will be higher when potatoes of high specific gravity are used. When potatoes are processed into chips, not only will the yield of chips be higher but there will be less absorption of frying oils. Chips with excessive oil content are classified as poor in quality and are usually more costly to produce. Investigations have shown that high specific gravity and mealiness are usually the cooking qualities most desired by the fresh consumer.

Other characters such as depth of tuber eye and smooth tuber appearance are important in that they eliminate waste in the preparation of potatoes for processed and fresh use. Tuber shape is also important; however, its value is determined by its specific use. Long shaped tubers are considered to be better for french frying and baking, while round shaped tubers are more suited for boiling. Round shaped tubers are especially adapted for mechanical peeling.

In most cases maturity and vigor are important to the overall worth of the variety. In order for a plant to manufacture carbohydrates efficiently, plant vigor becomes essential. Plant maturity is likewise important providing yield and other characters are properly maintained in the variety.

Each of these characters are dependent on hereditary factors, but the development of each character is influenced by environment which determines its varietal adaptation regardless of whether the most desirable genes are present. Generally no variety has been developed that will have the same qualities when grown under wide environmental conditions. It would be highly advantageous if potato varieties would express little difference in specific gravity when grown in the northern and southern parts of the United States. By having such varieties, processors and the fresh distributors would have varieties of more uniform quality over a longer period of time. Low variability for other important characters when grown over wider environmental conditions would also be highly beneficial.

Stevenson et al. (70) point out that specific gravity and most other characters are the end result of the interaction of hereditary factors or genes and of environment. The plant breeder can get new recombinations of genes and produce varieties that have a relatively high specific gravity when grown in a particular environment, but when grown elsewhere they might be much lower in specific gravity.

The success of any plant breeding program depends upon the presence of additive genetic variance within a population under selection. Heritability in the broad sense or the ratio of total genetic variance to total phenotypic variance can be used as a guide in determining the relative efficiency of selection. As heritability increases, the genetic component occupies an increasing portion of total variation and selection becomes more effective. In an asexually propagated crop, like potatoes, selection can be based on favorable additive dominance and epistatic gene combinations. Heritability estimates in the broad sense can be used to measure the efficiency of selection for future clonal generations and to calculate expected gain. The feasibility of selecting suitable gene recombinations from crosses involving parents with different character expression can improve the breeding and selection methods needed for the development of wider adapted varieties.

The purpose of this study was to determine what effect environment has on the genetic expression of certain characters found in the potato. The genetic variability of potato progenies grown in the northern and southern parts of the United States were studied with special emphasis placed on the character specific gravity. Concurrent studies were made on the characters plant maturity, vigor, tuber eye depth, tuber appearance, and tuber shape. Progeny from parents expressing wide differences in specific gravity and other characters were used in the study to determine if certain recombinations would be more beneficial in developing varieties showing little genetic variability when grown in the North and South. Heritability estimates and correlation coefficients were used to measure selection efficiency and character association and to determine if certain recombinations would show more genetic and less environmental effect. Clonal distribution and the amount of variability within a progeny line were also determined for clones grown in the North and South.

LITERATURE REVIEW

Several investigators (17; 28; 72) have shown that environment has a great influence on the genetic behavior of certain characters found in the Irish potato, Solanum tuberosum. Inherent differences in specific gravity of certain potato varieties grown over a wide range of environmental conditions have been reported by Stevenson and Whitman (72). Other workers (45) have found photoperiodism to have a great influence on the heritability of certain genetic characters of the Irish potato.

The literature concerning the cytogenetics and genetics of the Irish potato has been reviewed by Cadman (15) and others (56; 57; 60; 69; 71; 73). Cadman (15) reports that early workers generally accepted the phenomenon that the potato was a functional diploid. Recent investigators considered this to be rather unusual, as the Solanaceae family had long been a classical example of the polyploid series, and accurate counts of the somatic and gametic chromosome number of the potato were available as early as 1926 (15; 69). Cadman (15) further states the assumption that the potato was a diploid, survived unquestioned, until Lunden (43) published his comprehensive paper on tetraploidy in 1937.

Other workers such as Asseyeva and Nikolaeva (5) and Muller (46) had provided evidence, prior to 1937, for the occurrence of many duplicate factors suggesting tetrasomic inheritance. However, it was Lunden (43) who first obtained clear evidence of tetraploidy and showed that the potato was an autotetraploid--2N = 48 (69). Lunden (43) identified, among others, seven genes controlling color inheritance, five of which showed tetrasomic segregation. In recent years all

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The potato like most asexually produced crops has been found to be highly heterozygous for most characters and will segregate into different lines when self-pollinated (3: 71). However, pollen sterility has in many cases limited the possibility and amount of self-pollination (39).

Stevenson and Clark (71) point out that there are certain advantages and also certain disadvantages in using crosses between highly heterozygous material in a potato breeding program. One advantage would be that when both parents are heterozygous for the character under consideration, segregation will occur in the first generation, making it possible to obtain the desired recombination within the first generation. Another advantage would be that the individual from the progeny might be more vigorous than either parent. The main disadvantage of heterozygous material, according to Stevenson and Clark (71), would be the difficulty in obtaining exact genetic knowledge from the breeding material.

According to Rieman et al. (55), the asexually propagated clones used in most potato breeding programs were genotypes that segregate for most, if not all, of their important characters. They further reported that there are hundreds of genes influencing these characters and that these genes segregate in each cross. The magnitude and complexity of most potato breeding programs were also discussed.

Riedl (56) points out that there has been a comparative lack of knowledge concerning the breeding behavior of the most important characters of the potato that determines the true value of varieties for commercial production. He further states that most investigators in the past have preferred to deal with characters that can be distinguished accurately in all plants, such as qualitative characters, rather than with characters that are greatly dependent upon environmental conditions and can not be separated into discontinuous classes.

Much of the early work on the genetics of the potato was done by Krantz (38), Salaman (57), and others (5; 9; 10; 23; 33; 43; 46). However, Sirks (64) points out that compared with plants of equal economic importance the literature on potato genetics has been somewhat scarce and that it has also contained a number of peculiar cases. In some cases a certain character has appeared to be dominant and in other cases to be recessive (38; 57).

Krantz's results (38) obtained on inheritance of tuber shape agreed with those of Salaman (57) and indicated that shape depends on the presence or absence of a single factor for length. Salaman (57) suggested that plants may be either homozygous for long tubers, heterozygous for long tubers, or homozygous for round tubers. He showed that varieties with round tubers bred true for this character, giving progeny all with round tubers; while varieties with oval or long tubers will give long, oval, and round tubers (34; 59). However, Heribert (33) described a variety which did not breed true for roundness. This variety was assumed to have three polymeric factors controlling tuber shape, two of which were dominant for long.

Bartosch (9) studied the inheritance of tuber shape in progenies obtained from crosses and self-pollinations by measuring length/breadth coefficients. He found the F_1 to be intermediate between the two parents and that there was a positive correlation between tuber shape in the self-pollinated progenies and their parents. The distribution of tuber shape fitted, in many cases, the binomial curve. Swaminathan (73) suggested that these data could be explained by polymeric factors with at least four equal factor pairs being necessary. Bartosch (9) concluded that length was a constant character and that the different shapes were produced by a varying number of genes for roundness. Each additional gene for roundness increased the rate of growth in thickness. Similar results were reported by Black (11) who found that more than one gene controls tuber shape and that many round-tubered varieties appeared to be heterozygous for tuber shape.

Clark and Stevenson (18), working with inbred progenies of the variety Katahdin, found a wide range or variation in tuber shape. Some progenies were round like the variety Triumph while others were long and cylindrical like the variety Russet Burbank. These segregations indicated that at least part of the factors for tuber shape are carried by Katahdin in a heterozygous condition; however, according to Clark and Stevenson (18), a high percentage of short tuber types may be expected to be obtained when Katahdin is crossed with varieties having short tubers.

Clark and Stevenson (18) reported that one of the most outstanding characters of the variety Katahdin has been its shallowness of eyes. They found that when Katahdin was used as a parent its progeny had a very high percentage of tubers with shallow eyes.

Salaman (57; 58; 59) found that varieties with deeply incised eyes bred true for this character. However, he also found that hybrids were not completely dominant as both shallow and deep eyes were found on different tubers of the same variety. Heribert (33) and Salaman (58; 59) suggested that deep eyes were dominant to shallow eyes while East (23) obtained opposite results and showed that shallow eyes were dominant to deep eyes. Black (10) reported that deep eyes seemed to be recessive and were controlled by more than one gene.

Maturity has always been an important character of the potato. Krantz (38) found a wide range in time of maturity in the F_2 of a cross between two late-maturing varieties and showed that both parents were heterozygous for the factors determining time of maturity. Krantz (38) suggested that time of maturity was controlled by many genes. Salaman (59) reported that earliness was recessive and that early varieties bred true for earliness.

Blomquist and Lauer (12) grew sixteen progenies at two locations in Minnesota and studied seedling tuber size, maturity, tuber set, and tuber desirability. They found that the location by progeny interaction obtained for all characters were directly related to parent maturity. At one location the early-maturing parent clones performed better, whereas at the other location the late-maturing parents performed better.

Zubeldia (79), in recent work, has shown that certain techniques are helpful in selecting for earliness in the seedling stage. He found that early types may be obtained at an early stage of growth by selecting seedlings with an open-top foliage growth. Seedlings with a closed-top foliage growth are eliminated as they become late forms.

Specific gravity or the density of tubers is conditioned, like yield and other characters, by genetic factors (1; 68). Akeley and

Stevenson (1) reported that genetic segregation for specific gravity was evident when the comparisons were made within three family lines. Although tubers of the same seedling differed considerably in specific gravity, certain of the differences between seedlings of the same progeny were highly significant.

In another study on the inheritance of specific gravity, Akeley and Stevenson (2) selected and used five parents with wide differences in specific gravity. Specific gravity determinations were obtained for five clones, four selfed lines and eight crossed lines. The eight crossed lines represented various combinations of specific gravity such as high x high, high x medium, high x low, and medium x low. Their study showed that the two parents with the highest specific gravity gave the highest mean specific gravity for its progeny. This was followed in order by parents with specific gravity combinations of high x medium, high x low, and medium x low. Akeley and Stevenson (2) concluded that the five varieties were all heterozygous with respect to specific gravity, that high specific gravity seemed to be dominant over low specific gravity, and that although the number of genetic factors was not determined, multiple factors seemed necessary to explain their results.

In a recent study, Plaisted and Peterson (54) designed an experiment to find out if phenotypic recurrent selection could be used effectively to increase specific gravity. Two cycles of phenotypic recurrent selection were made from crosses involving five parents with high specific gravity. They found that an average gain of about 0.004 units of specific gravity of the second cycle over the first as measured in two seasons was significant beyond the .005 level. Results of seedling hill selection showed that small gains could be made, but that it was not consistent enough for general application to seedling selection. They concluded that where selection was for extremely high specific gravity, a moderate selection threshold would be generally effective.

Cunningham and Stevenson (21) reported on the inheritance of factors affecting potato chip color and their associations with specific gravity. They found that the heritability estimates for specific gravity were considerably lower than the estimates for chip color. This indicated that there was very little relationship between chip color and specific gravity and that these two characters are inherited independently. Seasonal effect also seemed to have a much greater effect on specific gravity than on chip color.

Like most other crops, environment has been found to have a great effect on the genetic heritability of many characters in the potato. According to Heinze and Craft (31), many factors such as rainfall, day length, temperature, sunlight, soil type, fertilizer, irrigation, fungicides, insecticides, and vine killers all have an effect on the specific gravity and other important characters of the potato. For example, Akeley and Stevenson (1) found relatively large differences in specific gravity of the same variety grown in the same field. The differences in specific gravity were still greater when the same variety was grown at different locations. They concluded that when a definite measurable character such as specific gravity varies so greatly in response to environmental conditions, it was not surprising that one variety was not equally adapted to all combinations of environment.

The literature contained many reports concerning the effect of environment on the specific gravity of the potato (28; 32; 49; 50; 51). Burton (14) reported that there was no simple evaluation of the effects of any one factor upon the specific gravity of the potato as length of day, temperature, rainfall, etc., but that all had a great effect.

Clark et al. (17), working in Maine, found a high coefficient correlation between specific gravity and the seasonal response of a wet and dry year. The dry season produced the highest specific gravity while the wet season produced the lowest specific gravity. Other workers (35; 50; 67) have reported that high amounts of rainfall or irrigation will lower the specific gravity of potatoes. However, Talburt and Smith (74) report that application of water often may result in a lower specific gravity, but that there are instances where the addition of water has actually raised the specific gravity. Apparently a water-soil temperature relationship occurred. If the season was extremely warm with high soil temperature, the water had a cooling effect resulting in higher specific gravity.

Further work on the effect of temperature on the specific gravity of potatoes has been reported by Kunkel et al. (40), who found that the specific gravity of potatoes increased until hot weather set in. After the temperature became warm, the vines began to die and the specific gravity decreased. Barrios (6) also found warm temperatures to lower the specific gravity of potatoes.

Bonde and Covell (13) found that specific gravity was lowered by any factor which caused premature death of the plant. Such factors were defoliation by the late blight disease and by insect infestation. They concluded that a good spray program would lengthen the season and result in higher specific gravity of the potato tubers. Similar results were reported by Murphy et al. (48) when they found that the influence of fungicides on specific gravity was caused by an increased maturity of the plant through their protection from defoliation diseases. In several instances they found certain fungicides to be more beneficial for increasing specific gravity.

Timm and Merkle (75) conducted field experiments in Pennsylvania to study the effect of the source of potassium on the specific gravity of potatoes. They found the specific gravity to be lowered when KCl was used in place of K_2SO_4. Similar results were reported by Laughlin (41) who found that both spray and soil applications of KCl reduced specific gravity.

Most investigators have possessed a widespread belief that a high degree of uniformity should exist in vegetatively propagated material (72). However, in contrast to this concept, several workers (61; 62) have reported a wide variation in the composition of individual tubers within the variety. Goldthwaite (26) concluded from his results that no two tubers, whether of the same variety or from the same plant, had exactly the same composition.

Stevenson and Whitman (72) measured the variability and attempted to determine what factors contribute to the variability found in a cooking test. Four popular varieties were grown at several locations and judged as to their cooking quality by a taste panel. Although they found the variability between variety and location to be high, certain varieties maintained a better quality than others over a wide range of conditions.

Several investigators have reported that photoperiodism has a great effect on the potato. Miller and McGoldrick (45), working in Louisiana, studied the effect of length of day on vegetative growth, maturity, yield, and smoothness of the potato grown under field and controlled conditions. They worked with different varieties grown under different photoperiods that were comparable to the spring and fall growing seasons in Louisiana. The spring season had eleven and one-half hours of daylight increasing to fourteen hours, and the fall season had fourteen hours of daylight decreasing to ten hours. The short days showed less vegetative growth, earlier maturity, and smoother tubers; while under the long days, the plants were more vegetative, matured later, and the tubers were deeper-eyed and more irregular in shape.

Early work by Garner and Allard (25) showed that a very long daylight period tends to direct the activities of the potato plant toward vegetative development to the exclusion of tuber set. Tincler (76) noted some varietal differences in the reaction to length of day, but in general he found the ratio of tops to tubers to be about seven times higher at thirteen hours than at ten hours. During the ten hours, there no doubt was a smaller proportion of the total production of carbohydrates being used for vine growth, which resulted in the surplus of carbohydrates being available for tuber formation (14).

Driver and Hawkes (22) investigated the reaction to length of day of certain species of Solanum. They found that these species varied widely in their response to day length. Maturity was hastened by short days at normal temperature, but under low temperature the reverse was true. Under a long day they found that it took over twice as long to mature as under a short day.

Edmundson (24) conducted a study with potatoes grown in the greenhouse at nine-, eleven-, and thirteen-hour photoperiods. He found that the different photoperiods had little effect on the diameter of the stem; however, he did find a significant difference in the height of the plants. The tallest plants were produced with the longest photoperiod.

The association between specific gravity of the raw potato tuber and the mealiness of the cooked product has been reported by several workers (16; 19; 61). Potato tubers of high specific gravity have in some cases given a characteristically mealy product, while those of low specific gravity have become watery or soggy when cooked. According to Shark (61), the association of high specific gravity and mealiness has been known since 1852. However, not all experimental evidence has supported this suggested relationship.

In general, the literature concerning the relationship between specific gravity and mealiness is controversial. Nylund and Poivan (52) and Unrau and Nylund (77) found that specific gravity of potato tubers provided a poor estimate of their cooking quality. They found potatoes of identical specific gravity to differ in mealiness. Nylund and Poivan (52) reported that the date of planting influenced the relationship between specific gravity and mealiness. Barrios (6) also found that date of planting, in addition to variety, influenced specific gravity and mealiness.

Other workers have found a discrepancy in the relationship of specific gravity and mealiness. Greenwood et al. (27) tested, by the sensory method, six varieties of potatoes grown on two farms in Connecticut and found that the varieties differed significantly from one another both in specific gravity and mealiness. They concluded that, in evaluating the mealiness of new varieties of potatoes, it would seem that sensory methods should be employed as well as specific gravity ratings until a more satisfactory objective method can be found.

Kirkpatrick et al. (37), working with four varieties of early-crop potatoes, found no significant correlation between specific gravity and mealiness in boiled, mashed, or baked potatoes. Such a correlation should have existed, they pointed out, since a significant correlation existed between specific gravity and dry matter, and between mealiness and dryness as determined by taste tests with boiled and mashed potatoes.

Barrios et al. (7) reported on variations in mealiness and chemical composition of southern-grown potatoes and tubers of the same varieties produced at a northern location. In this study mealiness was correlated with specific gravity, total starch, amylose and amylopectin. They found that specific gravity and mealiness were significantly correlated in tubers grown at southern locations during the spring season; however, they found no correlation between specific gravity and mealiness of the fall crop grown in either the South or the North. Factors other than specific gravity seemed to have a greater influence on mealiness as they found a definite correlation between mealiness and the per cent amylose and total starch. Amylose and total starch content were also highly correlated. They concluded that amylose content appeared to be a more objective method of predicting quality than either specific gravity or taste panel methods.

In another study the same investigators (8) attempted to correlate the possible variation in mealiness with the physical characteristics of the potato. In this study they reported on the relationship of cell size to specific gravity, mealiness, and starch content. They found tuber cell size to be significantly related to specific gravity and mealiness. Tubers of varieties containing the largest cells were rated highest in mealiness by a taste panel. Tuber cell size and starch content were also highly correlated, indicating that starch content was associated with cell size of tubers.

Even though most investigators found little or no correlation between specific gravity and mealiness, several workers reported some association and used specific gravity as a criterion for determining mealiness and good cooking quality of the potato. Cecil et al. (16) conducted a taste panel to determine consumers' response to the cooking quality of potatoes of high and low specific gravity. Their tests showed that high specific gravity had a highly significant effect on mealiness and sloughing. The potatoes of high specific gravity were more mealy and had a better flavor when baked, while potatoes of low specific gravity were less mealy and sloughed less when boiled.

Shark et al. (61) evaluated seven potato varieties by a taste panel of three judges to determine the relationship of specific gravity and mealiness of the cooked product. They found the differences between the seven varieties were significant when compared with mealiness scores of taste panels. However, Shark et al. (61) concluded that there were some factors other than specific gravity that influenced the evaluation of mealiness by the judges.

Other limitations concerning specific gravity are reported by Wittenberger (78), who found that the relationship between specific gravity and sloughing depended upon the physiological condition and storage history of the tubers. The extent of sloughing may decrease or increase without any change in specific gravity, or sloughing may even decrease as specific gravity increases. He concluded that any factor which decreases the amount of starch per cell, such as storage temperature, hastens the development of a less mealy texture.

Sharma et al. (62) reported on the differences in specific gravity within the three concentric zones of the potato tuber. The pith and the two outer zones of the tuber were studied. They found that potato varieties with high specific gravity had a characteristically higher specific gravity in the two outer zones, while potato varieties with low specific gravity expressed comparatively little differences in specific gravity between zones.

In another study, Sharma et al. (63) studied the influence of specific gravity and chemical composition on hardness of potato tubers after cooking. Potatoes that were firm or hard after cooking were generally characterized by a higher content of insoluble pectins and hemicelluloses and were higher in specific gravity.

Sistrunk et al. (65) found little relationship between specific gravity, chip color, and mealiness of potatoes grown in Louisiana. However, Lyman and Mackey (44), working in Oregon, found a definite correlation between chip color and specific gravity. Tubers of higher specific gravity consistently produced chips of lighter color than did tubers of lower specific gravity.

MATERIALS AND METHODS

Description of Material

Experiments were designed to determine the effect of environment on the phenotype of certain heritable characters found in the Irish potato, Solanum tuberosum. The genetic variability of first and second clonal generations grown in the southern and northern parts of the United States was studied. Special emphasis was placed on specific gravity. Concurrent studies were also made on phenotypic variability of plant maturity, vigor, tuber shape, tuber eye depth, and tuber appearance.

Ten potato progeny lines developed from one self-pollination and nine cross pollinations were grown at Baton Rouge, Louisiana, and at Grand Forks, North Dakota. Tubers of these progeny lines were planted and harvested at the Ben Hur Experimental Farm, Baton Rouge, Louisiana, in 1963 and at the Potato Research Farm, Grand Forks, North Dakota, during 1962 and 1963. Pedigree numbers and parents of the ten family lines which produced progenies for testing are given in Table 1.

Twelve parents which represented a wide range of horticultural characters were used in this study. Table 2 shows the mean specific gravity and numerical rating of the twelve parents grown in Louisiana and North Dakota. Parents were selected which represented a wide range in specific gravity as well as wide differences in other horticultural characters (Tables 2 and 3).

Nine of the parents chosen were named varieties while three were advanced clonal selections. Irish Cobbler, Katahdin, and White Rose

TABLE 1. Pedigree number, parentage, and number of clones planted and harvested at Baton Rouge, Louisiana, and Grand Forks, North Dakota, 1962-1963

Pedigree number	Parentage	First clonal generation grown in N. Dak., 1962: No. of clones planted	First clonal generation grown in N. Dak., 1962: No. of clones harvested	Second clonal generation grown in La. and N. Dak., 1963: No. of clones planted	Second clonal generation grown in La. and N. Dak., 1963: No. of clones harvested
1	Early Gem x Katahdin	186	125	125	116
2	La Chipper x Katahdin	177	110	110	73
3	Irish Cobbler x Katahdin	180	130	130	120
4	White Rose x Katahdin	146	91	91	65
6	Katahdin selfed	48	31	31	13
7	Bounty x ND 4524-16R	130	100	100	66
8	Bounty x ND 4524-7R	140	100	100	62
9	Bounty x Viking	130	100	100	77
10	Norland x TL 1859	130	100	100	68
11	Catoosa x Norland	99	65	65	50
Total		1,366	952	952	710

TABLE 2. Specific gravity reading and numerical ratings of the twelve parents grown in Louisiana and North Dakota during 1963

Parent	Specific gravity		Plant maturity[a]		Vigor[b]		Tuber shape[c]		Tuber eye depth[d]		Tuber appearance[e]	
	N.D.	La.	N.D.	La.	N.D.	La.	N.D.	La.	N.D.	La.	N.D.	La.
Bounty	1.083	1.059	4	4	5	3	3	4	3	4	4	3
Catoosa	1.076	1.059	2	3	3	2	4	4	4	4	2	4
Irish Cobbler	1.090	1.079	2	1	2	1	3	1	2	2	2	3
Early Gem	1.078	1.057	1	1	2	2	4	5	4	3	3	3
Katahdin	1.089	1.058	4	4	3	3	2	4	3	4	3	4
La Chipper	1.094	1.070	2	2	3	3	1	1	2	3	4	4
Norland	1.071	1.058	1	1	2	1	4	4	4	4	4	4
Viking	1.093	1.062	3	3	3	3	4	4	4	4	3	4
White Rose	1.080	1.060	3	3	4	4	7	7	4	4	2	3
ND 4524-7R	1.083	1.057	3	3	3	4	2	1	4	4	4	4
ND 4524-16R	1.098	1.072	4	4	5	4	4	1	3	4	4	4
TL 1859	1.092	1.054	4	3	4	3	6	4	3	4	2	3
Mean	1.086	1.062	2.8	2.7	3.3	2.8	3.7	3.3	3.3	3.7	3.1	3.6

[a]1 = very early; 5 = very late.

[b]1 = very poor; 5 = extreme vigor.

[c]1 = round; 7 = long.

[d]1 = deep; 5 = very shallow.

[e]1 = very poor; 5 = good appearance.

TABLE 3. Mean specific gravities and numerical ratings of parents grown in Louisiana and North Dakota during 1963[a]

Pedigree number	Parentage	Specific gravity		Plant maturity[b]		Vigor[c]		Tuber shape[d]		Tuber eye depth[e]		Tuber appearance[f]	
		N.D.	La.	N.D.	La.	N.D.	La.	N.D.	La.	N.D.	La.	N.D.	La.
1	Early Gem x Katahdin	1.084	1.058	2.5	2.5	2.5	2.0	3.0	4.5	3.5	3.5	3.0	3.5
2	La Chipper x Katahdin	1.092	1.064	3.0	3.0	3.0	3.0	1.5	2.5	2.5	3.5	3.5	4.0
3	Irish Cobbler x Katahdin	1.090	1.069	3.0	2.5	2.5	2.0	2.5	2.5	2.5	3.0	2.5	3.5
4	White Rose x Katahdin	1.085	1.059	3.5	3.5	3.5	3.5	4.5	5.5	3.5	4.0	2.5	3.5
6	Katahdin selfed	1.089	1.058	4.0	4.0	3.0	3.0	2.0	4.0	3.0	4.0	3.0	4.0
7	Bounty x ND 4524-16R	1.095	1.066	4.0	4.0	5.0	3.5	3.5	2.5	3.0	4.0	4.0	3.5
8	Bounty x ND 4524-7R	1.083	1.058	3.5	3.5	4.0	3.5	2.5	2.5	3.5	4.0	4.0	3.5
9	Bounty x Viking	1.088	1.061	3.5	3.5	4.0	3.0	3.5	4.0	3.5	4.0	3.5	3.5
10	Norland x TL 1859	1.082	1.059	2.5	2.0	4.5	3.0	5.0	4.0	3.5	4.0	3.0	3.5
11	Catoosa x Norland	1.074	1.059	1.5	2.0	2.5	2.0	4.0	4.0	4.0	4.0	3.0	4.0

[a]Mid-parent value for each parental recombination.

[b]1 = very early; 5 = very late.

[c]1 = very poor; 5 = extreme vigor.

[d]1 = round; 7 = long

[e]1 = deep; 5 = very shallow.

[f]1 = very poor; 5 = good appearance.

were well established varieties of rather old origin while Bounty, Catoosa, Early Gem, La Chipper, Norland, and Viking were of relatively new origin. ND 4524-7R and ND 4524-16R were advanced sister selections from North Dakota State University's breeding program, while TL 1859 was an advanced clonal selection from the United States Department of Agriculture, Louisiana State University's breeding program.

Crosses made and progeny derived from these parents represented specific gravity combinations of high x high, high x medium, high x low, medium x medium, medium x low, and low x low. In addition, parental varieties produced progeny that represented different recombinations of plant maturity, vigor, tuber shape, tuber eye depth, and tuber appearance.

Experimental Procedures

Greenhouse Seedlings Grown in Louisiana and North Dakota

Potato seedling tubers were produced from true potato seed grown at Louisiana and North Dakota State Universities. True potato seed derived from cross- and self-pollinations had previously been harvested in the field at Louisiana State University and in the greenhouse at North Dakota State University. In order to obtain all different parental recombinations needed for this study, it was necessary to grow five seedling families at each location.

True potato seed were planted in seedling flats containing vermiculite in August, 1961, in the greenhouse at Louisiana State University. The potato seedlings were transplanted into 3-inch clay pots in early September. On January 4 and 5, 1962, after proper tuber size had been achieved, one to four seedling tubers from each plant were harvested and saved separately within family lines. Seedling tubers from all family lines were identified and stored at 40° F. until April and then shipped to North Dakota State University for planting.

True potato seed were planted in seedling flats containing well-mixed potting soil during July, 1961 in the greenhouse at North Dakota State University, and the seedlings were subsequently transplanted into 3-inch clay pots on August 1. On November 2 and 3, after proper tuber size had been achieved, all seedling plants were harvested and saved separately. All tubers harvested were properly identified and stored at 40° F. until spring planting.

First-Year Clonal Generation Grown at Grand Forks, North Dakota, 1962

In the spring of 1962 the first field planting of the ten family lines was made at Grand Forks, North Dakota. Greenhouse seedling tubers that had previously been grown at Louisiana State University and North Dakota State University were planted as separate clonal lines on June 12, 1962. Seedling tubers were planted with an assisted feed potato planter. Three hundred pounds of 16-16-8 fertilizer were applied in the furrow at planting time.

Seedling families were planted in blocks. Each seedling tuber was spaced 1 foot within the row and 3 feet between rows. Seedling tubers representing the first clonal generation were placed 5 feet between each progeny line. During the growing season, regular applications of insecticides and fungicides were applied by a high-pressure sprayer.

Several clones were lost during the growing season (Table 1).

This loss or reduction in number at harvest was attributed to poor or no tuberization and general loss during the season.

On September 25, 1962, the vines were removed by roto-beating, and on October 1 all clones were harvested by a single-row, level-bed, tractor-driven potato digger. Nine hundred and fifty-two clones representing the ten family lines were harvested and saved separately.

Following harvest, records were taken on specific gravity, tuber shape, eye depth, and tuber appearance. Specific gravity was determined by the salt brine method (49). The potato hydrometer was not used because most clones lacked the 8 pounds of tubers needed for its calibration. Data concerning tuber shape, tuber eye depth, and tuber appearance were taken by a standard rating scale devised for this study.

After all necessary data were recorded, two to three tubers from each clone were shipped to Baton Rouge, Louisiana, for planting during January, 1963. The remainder of all clones were stored at the University of North Dakota until planting in early May, 1963.

Although 952 clones were harvested, only those clones which were represented in all tests were included in the statistical analyses and tables.

Second Clonal Generation Grown at Baton Rouge, Louisiana, 1963

On January 29, 1963, nine hundred and fifty-two clones derived from first clonal generation grown in North Dakota were planted at Baton Rouge, Louisiana. Each of the clones was to have been represented by an eight-hill clonal plot; however, due to damage of the tuber seed by freezing, some of the clones were not represented by eight hills. The plot was planted by hand with each tuber spaced approximately 1 foot within the row and 4 1/2 feet between rows. The 952 clonal lines were spaced approximately 3 feet apart with each of the ten progeny lines planted in blocks. The twelve parental varieties used in this study were planted adjacent to the clonal blocks.

Four applications of irrigation water representing approximately 4 inches of water were applied to the plot during the season. Regular applications of fungicides and insecticides were made to control fungus diseases and insects.

On May 29, 1963, plant maturity and vigor readings were recorded for all clones. Clones were rated for plant maturity and vigor using a numerical rating scale. On May 30 and 31 the plot was harvested by the use of a tractor-driven potato digger, common to that area. Seven hundred and ten clones survived this test and were harvested and saved separately (Table 1). Immediately following harvest, specific gravity was taken on all clones with a potato hydrometer. The weight in water and air method was used only when samples lacked the required 8 pounds needed for the hydrometer test. Several investigators (49; 66) have reported that both tests are comparable and adequate for specific gravity determinations. Concurrent readings were taken on tuber shape, tuber eye depth, and tuber appearance.

Second Clonal Generation Grown at Grand Forks, North Dakota, 1963

On May 7, 1963, nine hundred and fifty-two second clonal generations representing the ten progeny lines were planted at Grand Forks, North Dakota. All clones planted were identical to the clones grown at Baton Rouge, Louisiana. Planting was made by the use of an Iron-Age assisted feed potato planter, with 200 pounds of 16-16-8 fertilizer applied in a band form. Each clone was represented by an eight-hill plot with each tuber planted 1 foot apart within the row and 3 feet between rows. The ten progeny lines were planted in blocks with approximately 4 feet separating each clone. Parental varieties were planted adjacent to clonal blocks.

The plot was sprayed regularly with fungicides and insecticides to control diseases and insects during the growing season.

Plant maturity and vigor readings were recorded on August 20 and 21, 1963. Vine growth was eliminated by roto-beating on September 13. The plot was harvested by a single-row, level-bed, tractor-driven potato digger on September 13 and 14. Nine hundred and twenty clones survived this test and were harvested. Data were recorded on those clones that survived the test when grown at Baton Rouge, Louisiana. Following harvest, specific gravity readings were taken with a potato hydrometer. Again, the weight in water and air method was used when the 8 pounds required for the hydrometer were lacking. Readings were also recorded for tuber shape, tuber eye depth, and tuber appearance.

Collection of Data

Specific Gravity

Specific gravity determinations were made by the potato hydrometer method (66), weight in water and air (49), and by the salt brine method (49). All of these methods have been considered accurate and rapid for determining the specific gravity of potatoes (49). The potato hydrometer method consisted of weighing 8 pounds of tubers from each sample. Weighed samples were then placed in a wire basket that was suspended from a bulb attached directly to the hydrometer. The sample and apparatus were placed in a container of water and the specific gravity was read directly from the scale on the hydrometer tube.

The salt brine method consisted of preparing a series of NaCl solutions of known densities. Tubers from each sample were moved from the low-density solution through the series of high-density solutions. The specific gravity of a given potato sample was that of the solution where the tubers remained suspended. Density of all tubers in each sample was averaged and recorded as specific gravity.

Specific gravity determined from weight in air and water was derived from the following formula:

$$\frac{\text{Weight in air}}{(\text{Weight in air}) - (\text{Weight in water})} = \text{Specific gravity}$$

Plant Maturity and Vigor

Prior to harvest, vine maturity and plant vigor readings were recorded individually on all second generation clones grown in Louisiana and North Dakota. An average numerical rating was recorded for each clone by comparing the clones with certain standard parental varieties included in this study.

The following rating scales were used for vine maturity and plant vigor:

Plant maturity		
Rating scale	Maturity	Comparable to
1	Very early	Norland
2	Early	Cobbler
3	Medium	Viking
4	Late	Katahdin
5	Very late	

Vigor		
Rating scale	Vigor	Comparable to
1	Very poor	Norland
2	Poor	Early Gem
3	Medium	Viking
4	Good	White Rose
5	Extremely vigorous	Bounty

Tuber Shape, Tuber Eye Depth, and Tuber Appearance

Determinations of tuber shape, tuber eye depth, and tuber appearance were recorded on the same sample of tubers used for specific gravity readings. Tuber shape was determined on all clones by an arbitrary rating scale of 1 to 7. The extreme variability existing within a sample made it necessary to establish seven different classifications. Tubers that were round were given a numerical rating of 1; round-oblong--2; oblong-round--3; oblong--4; oblong-long--5; long-oblong--6; and long tubers--7. Numerical rating for each clone was established by a composite sample with the greatest number of tubers falling into a definite class.

Tuber eye depth was determined by rating scale of 1 to 5. Tubers with deeply incised eyes were given a rating of 1; deep eyes--2; medium eyes--3; shallow eyes--4; and very shallow eyes, which were highly superficial, a rating of 5.

Tuber appearance was rated on a scale of 1 to 5, with 5 being highly superior or desirable. Other numerical ratings were as follows: 1--very poor; 2--poor; 3--average; and 4--good appearance. Clones having a rating of 1 and 2 would have no possibilities as a commercial variety while clones having a rating of 4 or 5 were considered as potential variety material. Tuber appearance was based on a composite rating that involved all the aspects concerned for good horticultural characters.

Weather Data

At Baton Rouge, Louisiana, and Grand Forks, North Dakota, temperatures were recorded by a standard hygrothermograph and precipitation by a standard rain gauge. Daily air temperatures were recorded shortly after planting and were continued until the potatoes were harvested. At Baton Rouge, approximately 1 inch of irrigation water was applied four times during the season. No irrigation facilities were available for the plot grown at Grand Forks, North Dakota. Maximum and minimum temperatures taken every week following planting in 1963 are shown in Figure 1.*

Statistical Analyses

Calculations

Mean, standard deviation, correlation coefficient, standard error of correlation coefficient, and variance components were computed with the IBM 1620 computer. Coefficient of variability, expected mean square, estimate of variance components, heritability, and expected genetic selection advance were computed by the use of a standard calculator.

Heritability, in the broad sense which considers total genetic variability in relation to the phenotypic variability, was used to estimate heritability. Variance was separated into three components—location, clones, and clones by location. Plot heritability, in the broad sense, was based on the models used by Hanson et al. (30) and Mullins (47). Clonal heritability used to predict selection advance in the next clonal generation was based on the model by Allard (3) and Mullins (47).

Total variance for specific gravity, plant maturity, vigor, tuber eye depth, and tuber appearance were separated into three sources

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*Figures 1 through 10 are shown in the Appendix.

of variability--locations, clones, and clones by location. Estimates of variance components were obtained for each progeny line and for each character. Calculations were made as follows:

Source of variation	d.f.	Mean square	Expected mean square
Location	(L-1)	M_1	$\sigma^2_C \times L + \sigma^2_L$
Clones	(C-1)	M_2	$\sigma^2_C \times L + \sigma^2_C$
Clones x location	(C-1)(L-1)	M_3	$\sigma^2_C \times L$

The estimated variance components for clones =

$$\frac{\text{Mean square for clones} - \text{mean square for clones x location}}{2}$$

The estimated variance components for clones x location = mean square for clones x location.

Clonal heritability to predict selection advance was computed by the formula and model presented by Allard (3) and Mullins (47):

GS = (K) x (σA) x (H).

GS = The expected genetic advance under selection.

(K) = Selection differential expressed in units of standard deviation assuming normal distribution of observation. According to Allard (3), if the highest 10.0 per cent of clones are saved K takes a value of 1.76.

(H) = Clonal heritability

$$\frac{\sigma^2_C}{\sigma^2_C + \frac{\sigma^2_C \times L}{2}} \times 100 = \text{clonal heritability}$$

σ^2 is the estimated variance component for clones.

$\sigma^2_C \times L$ is the estimated variance component for clones x location.

(σA) = Phenotypic standard error

$$\sqrt{\sigma^2_C + \frac{\sigma^2_{C\ x\ L}}{2}}$$

Hanson et al. (30) discussed the use of a formula for which interaction components were not divided by the number of locations, years, or replications involved. According to Hanson et al. (30), this was more appropriate when comparing heritability estimates for different characters and from different experiments. This method was referred to as heritability of single plots (30; 36; 47). The estimates of variance components for each progeny line and for each character were the same as those calibrated for clonal heritability. The following formula was used to estimate heritability on a single-plot basis for all characters in this study:

$$\frac{\sigma^2_C}{\sigma^2_C + \sigma^2_{C\ x\ L}} \times 100 = \text{heritability on a single-plot basis}$$

σ^2_C is the estimated variance component for clones.

σ^2_C x L is the estimated variance component for clones x location.

Coefficients of correlation were obtained for all characters both within and between locations.

EXPERIMENTAL RESULTS

This study was designed to determine the effect of environment on specific gravity, plant maturity, vigor, tuber shape, tuber eye depth, and tuber appearance when potato progenies were grown in the South and in the North. Results from this study represent data collected from the following sources: (a) potato progenies grown as first clonal generations in North Dakota; (b) potato progenies grown as second clonal generations in both Louisiana and North Dakota. Results are presented in three parts: (a) character expression; (b) correlation and association; and (c) heritability.

Character Expression

Specific Gravity of First-Year Clonal Generation Grown in North Dakota, 1962

Table 4 shows the frequency distribution, mean, standard deviation, and coefficient of variability for specific gravity of the ten progeny lines grown at Grand Forks, North Dakota, in 1962. The means of all progenies ranged from 1.063 to 1.075 indicating that some differences existed between progenies. The standard deviation, which is the measure of variability within the progeny line, ranged from 4.50 (.001) to 6.79 (.001) units. Coefficient of variability, which is the ratio of standard deviation of the sample mean, ranged from 7.2 to 10.1 per cent. According to LeClerg et al. (42), coefficient of variability affords a relative measure of dispersion so that variation may be compared in features expressed in different units of measurement.

TABLE 4. Frequency distribution, mean, standard deviation, and coefficient of variability for specific gravity of the ten progeny lines grown in North Dakota during 1962

Pedigree number	Distribution of clones in specific gravity classes										No. clones	Mean	Std. dev.[a]	% coef. var.
	Below 1.054	1.059 1.061	1.062 1.064	1.065 1.067	1.068 1.070	1.071 1.073	1.074 1.076	1.077 1.079	1.080 1.082	Above 1.082				
1	14	16	19	22	22	8	7	3	3	2	116	1.066	6.43	9.5
2	1	9	9	9	9	15	11	5	2	3	73	1.070	6.75	9.7
3	1	4	8	17	21	23	16	19	4	7	120	1.072	6.55	9.0
4	15	14	20	6	5	4	1				65	1.063	4.50	7.2
6	1	2	1	2	2	2	2	0	1	0	13	1.068	6.87	10.1
7	0	1	4	3	7	11	14	10	5	11	66	1.075	6.79	9.0
8	2	3	5	9	10	9	9	9	3	3	62	1.071	6.50	9.1
9	2	2	4	12	11	14	20	4	5	3	77	1.072	6.01	8.4
10	1	1	1	7	5	12	11	14	9	7	68	1.075	6.26	8.3
11	1	0	3	5	10	7	8	9	6	1	50	1.073	6.02	8.2
Total	38	52	74	92	102	105	99	73	38	37	710			
Mean												1.075	6.27	8.8

[a]Specific gravity coded by (.001). Standard deviation calculated on individual measurements.

The differences found within each family indicated genetic segregation for specific gravity. This genetic segregation varied a great deal between family lines and showed that parents were highly heterozygous for specific gravity.

The progeny lines involving two parents of high specific gravity, Pedigree No. 7, Bounty x ND 4524-16R, produced progeny of the highest mean specific gravity. This particular progeny line had 16.4 per cent of its population having a specific gravity reading above 1.082 and only 12.0 per cent of its population below 1.067. The progeny lines from Pedigree Nos. 1 and 4 involving Katahdin x Early Gem and Katahdin x White Rose produced the lowest progeny means. Katahdin and White Rose are considered medium specific gravity parents while Early Gem is considered to be very low. Pedigree Nos. 1 and 4 had 61.3 per cent and 84.6 per cent, respectively, of their total progeny below 1.067.

Pedigree Nos. 1, 2, 3 and 8, which were crosses between low x medium, high x medium, and high x low, showed a high degree of segregation for specific gravity. Akeley and Stevenson (2) reported similar results when two varieties, one medium and the other low in specific gravity, were crossed.

The number of genetic factors involved was not determined in this study; however, evidence of multiple factors was quite evident with several crosses (Table 4). Pedigree Nos. 7, 8, and 9 involving Bounty x ND 4524-16R (high x high), Bounty x ND 4524-7R (high x low), and Bounty x Viking (high x medium) showed evidence of multiple genetic effect (Table 4). Several other crosses expressed similar results.

Specific Gravity of Second Clonal Generations

Grown in Louisiana and North Dakota, 1963

Tables 5 and 6 show the frequency distribution, mean, standard deviation and coefficient of variability for specific gravity of second clonal generations grown in Louisiana and North Dakota. This was a duplicate of similar clones grown in North Dakota in 1962.

Parent varieties expressed inherent differences in specific gravity (Table 2). ND 4524-7R with 1.057 and Irish Cobbler with 1.079 had the lowest and highest specific gravities when grown in Louisiana.

Standard deviations in Louisiana showed a range of 3.11 to 5.99 (.001) units of specific gravity while coefficient of variability ranged from 5.1 to 9.6 per cent for all progeny lines (Table 5). Standard deviation and coefficient of variability indicated that a relatively low degree of variability in specific gravity occurred with progeny lines. The mean specific gravity reading between family lines ranged from 1.058 to 1.062, which also indicated that a low degree of variability existed between family lines (Table 5).

Even though variability between and among family lines was low, several progeny lines showed some degree of segregation for specific gravity. Results were comparable to progeny from the first clonal generation grown in North Dakota in 1962. Segregation for specific gravity was high when parents of low x high, high x medium, and low x medium were used.

Pedigree No. 7 involving Bounty x ND 4524-16R (high x high) had 16.6 per cent of its total progeny having a specific gravity reading over 1.068. Pedigree No. 11, which had two low specific gravity parents,

TABLE 5. Frequency distribution, mean, standard deviation, and coefficient of variability for specific gravity of the ten progeny lines grown in Louisiana during 1963

Pedigree number	Distribution of clones in specific gravity classes: Below 1.050	1.050 1.052	1.053 1.055	1.056 1.058	1.059 1.061	1.062 1.064	1.065 1.067	1.068 1.070	1.071 1.073	Above 1.073	No. clones	Mean	Std. dev.[a]	% coef. var.
1	4	2	1	34	47	17	8	2	0	1	116	1.059	4.82	8.1
2	1	2	0	12	26	10	10	7	5	0	73	1.062	5.23	8.4
3	1	0	0	27	35	26	16	10	4	1	120	1.062	4.36	7.0
4	2	2	1	22	26	8	4	0	0	0	65	1.059	3.66	6.2
6	1	0	0	3	7	1	1				13	1.059	3.73	6.3
7	4	0	0	9	21	11	10	9	1	1	66	1.062	5.99	9.6
8	4	2	0	23	25	4	1	1	1	1	62	1.058	5.62	9.6
9	2	0	0	18	28	10	10	6	2	1	77	1.061	4.85	7.9
10	1	0	0	18	23	16	4	4	1	1	68	1.061	4.68	7.6
11	0	0	1	23	14	7	5				50	1.061	3.11	5.1
Total	20	8	3	189	252	110	69	39	14	6	710			
Mean												1.060	4.60	7.6

[a]Specific gravity coded (.001). Standard deviation calculated on individual measurements.

TABLE 6. Frequency distribution, mean, standard deviation, and coefficient of variability for specific gravity of the ten progeny lines grown in North Dakota during 1963

Pedigree number	Distribution of clones in specific gravity classes: Below 1.071	1.071 1.073	1.074 1.076	1.077 1.079	1.080 1.082	1.083 1.085	1.086 1.088	1.089 1.091	1.092 1.094	Above 1.094	No. clones	Mean	Std. dev.[a]	% coef. var.
1	5	2	7	10	18	21	18	12	10	13	116	1.085	7.78	9.1
2	2	0	1	0	3	7	17	16	12	15	73	1.090	6.21	6.9
3	1	0	3	3	7	17	14	20	24	31	120	1.090	6.70	7.4
4	5	1	2	3	10	16	12	7	5	4	65	1.084	7.61	9.0
6			1	0	0	3	1	2	1	5	13	1.091	7.64	8.4
7	1	0	2	1	7	14	10	8	13	10	66	1.088	6.67	7.5
8	6	5	3	5	9	13	9	10	1	1	62	1.082	7.57	9.2
9	1	2	5	4	6	20	12	11	8	8	77	1.086	6.46	7.5
10	3	1	3	12	7	14	11	8	8	1	68	1.084	6.65	7.9
11	1	2	4	8	10	8	8	5	4	0	50	1.082	5.99	7.2
Total	25	13	31	46	77	133	112	99	86	88	710			
Mean												1.086	6.90	8.0

[a]Specific gravity coded (.001). Standard deviation calculated on individual measurements.

Norland and Catoosa, did not produce any progeny that averaged over 1.068 in specific gravity. This again showed that although environment did influence specific gravity, genetic influence becomes important when parents of different specific gravity were used.

Progeny means of family lines differed by zero to seven specific gravity intervals lower than the means of their respective mid-parent values. In comparison to the low amount of variability between and within family lines, the variability between certain progeny and parents might be considered quite great. The greatest mean difference between parents and progeny was found with Pedigree No. 3, Irish Cobbler x Katahdin, which was seven specific gravity intervals lower than the mean of their parents (Tables 3 and 5).

Table 6 gives the frequency distribution, mean, standard deviation, and coefficient of variability for specific gravity of second-year clonal lines in North Dakota. Progeny means ranged from 1.082 to 1.091, standard deviation 5.99 to 7.78 (.001) units, and coefficient of variability 6.9 to 9.2 per cent. Standard deviation and coefficient of variability for specific gravity were found to be quite similar to previous tests.

Wide differences in specific gravity were found among parental varieties grown at Grand Forks (Table 2). ND 4524-16R and Norland with 1.098 and 1.071, respectively, had the highest and lowest specific gravity.

For second clonal generation grown in North Dakota, segregation for specific gravity was evident for most all progenies, which again indicated a high degree of heterozygosity for that character. There was a higher degree of variability for specific gravity within all families and a wider difference between progeny families (Table 6). In general, environmental conditions in North Dakota during 1963 were conducive to the production of high specific gravity.

Progeny from Pedigree lines 2, 3 and 7, involving crosses of high x high and high x medium parents, had the highest mean specific gravity. Sixty-two and one-half per cent of the progeny from Pedigree No. 3, Irish Cobbler x Katahdin (high x medium), gave specific gravity readings over 1.089. Fifty-eight and eight-tenths of the progeny in Pedigree No. 2, La Chipper x Katahdin (high x medium), was over 1.089 in specific gravity, while Pedigree No. 7, Bounty x ND 4524-16R (high x high), and Pedigree No. 9, Bounty x Viking (high x medium), produced 47.0 per cent and 35.1 per cent, respectively, of their total progeny over 1.089 in specific gravity. Genetic influence was again evident with Pedigree No. 11, Catoosa x Norland (low x low), which produced the lowest mean specific gravity. Only 18.0 per cent of its total progeny averaged over 1.089 per cent in specific gravity.

In most cases, the progeny mean of the family lines equalled the average specific gravity of the two parents involved in the cross. The progeny mean of most family lines differed by zero to two intervals lower or higher than the mean of its parents (Table 3). Pedigree Nos. 7 and 11 differed by six and nine specific gravity intervals, respectively, from the means of their clonal parents (Tables 3 and 6).

<u>Plant Maturity of Second Clonal Generations Grown in Louisiana and North Dakota, 1963</u>

Table 7 shows frequency distribution, mean, standard deviation, and coefficient of variability for plant maturity of second-year clonal generations grown in Louisiana and North Dakota. Mean maturity of

TABLE 7. Frequency distribution, mean, standard deviation, and coefficient of variability for plant maturity of the ten progeny lines grown in Louisiana and North Dakota during 1963

Pedigree number	Location	Distribution of clones in maturity classes[a] 1	2	3	4	5	Total clones	Mean	Std. dev.	% coef. var.
1	Louisiana	9	31	41	31	7	119	2.98	1.025	37.4
	North Dakota	7	20	30	38	24	119	3.44	1.154	33.5
2	Louisiana	8	27	27	11	0	73	2.56	.876	34.1
	North Dakota	8	13	21	30	1	73	3.04	1.039	34.2
3	Louisiana	19	52	30	18	1	120	2.41	.954	39.5
	North Dakota	9	21	31	40	19	120	3.32	1.156	34.8
4	Louisiana	5	25	21	11	3	65	2.72	.985	36.2
	North Dakota	2	10	17	26	10	65	3.49	1.024	29.3
6	Louisiana	1	5	4	3	0	13	2.69	.947	35.2
	North Dakota	1	0	4	5	3	13	3.69	1.109	30.1
7	Louisiana	6	26	19	12	5	68	2.74	1.077	39.3
	North Dakota	4	18	25	16	5	68	3.00	1.015	33.8
8	Louisiana	3	28	18	11	7	67	2.77	1.053	38.0
	North Dakota	4	24	19	12	8	67	2.90	1.117	38.5
9	Louisiana	14	28	17	17	11	87	2.80	1.165	44.9
	North Dakota	13	17	27	18	12	87	3.00	1.174	41.3
10	Louisiana	29	20	11	11	1	72	2.09	1.134	54.2
	North Dakota	13	31	15	12	1	72	2.38	.940	39.4
11	Louisiana	25	19	7	3	1	55	1.68	.786	46.7
	North Dakota	7	26	13	7	2	55	2.36	.911	38.6
Mean	Louisiana							2.54	1.000	40.6
	North Dakota							3.06	1.064	35.4

[a] 1 = very early maturity
2 = early maturity
3 = medium maturity
4 = late maturity
5 = very late maturity.

parents involved in this study are found in Table 2.

Inherent differences in maturity were found in parental varieties grown in Louisiana and North Dakota (Table 2). Maturity classification among parental varieties was evenly distributed. The twelve parents were either very early, early, medium, or late in maturity. Wide differences in parental maturity allowed the progenies of the following crosses to be studied: very early x early, early x medium, early x late, medium x medium, and late x late.

In Louisiana, progeny means for maturity of the family lines ranged from 1.68 to 2.98 units, standard deviation .786 to 1.165 units, coefficient of variability 34.1 to 54.2 per cent. This coefficient of variability was much higher than that for specific gravity. The mean of all ten family lines studied had 16.1 per cent of its total progeny in the very early maturity class, 35.3 per cent in the early class, 26.4 per cent in the medium class, 17.3 per cent in the late class, and 4.9 per cent in the very late maturity class (Figure 2). This indicated that parents were highly heterozygous for maturity and that segregation within families was quite high. The relatively high coefficient of variability also indicated the high degree of progeny variability within a family line (Table 7).

Genetic influence was evident when family lines involving parents of different maturity classifications were crossed (Figure 7). Progeny from Pedigree No. 11, Catoosa x Norland (early x very early), had 79.9 per cent of its total progeny in very early to early maturity classes. With Pedigree No. 8, Bounty x ND 4524-7R (late x late), only 46.3 per cent of its total progeny fell into a very early or early class.

Although the highest percentage of clones from all families were in the early to medium maturity class, the late x late parents produced the highest percentage in the late to very late classes. In most cases the progenies from the early x early and early x medium crosses equalled the mean of their respective parents. However, this was not true when late x medium or late x late parents were used.

In North Dakota, the maturity means for the progeny lines were 2.36 to 3.69 units with standard deviations of .911 to 1.174 and coefficients of variability of 29.3 per cent to 41.3 per cent. Coefficient of variability was found to be lower than that in Louisiana; however, it was still considered to be statistically high (Table 7). Frequency distribution again showed a relatively wide range; however, comparing this to the Louisiana trial, more clones were in the late to very late and less in the very early to early classes. This was due to the effect of environment on maturity. Figure 2 shows the mean clonal distribution of all ten progeny lines. Nine and two-tenths per cent of the progeny were very early, 24.3 per cent early, 27.3 per cent medium, 27.6 per cent late, and 11.5 per cent were very late.

When clones were grown in North Dakota, gene expression also seemed quite apparent (Figure 7). Although parents were highly heterozygous for maturity, gene influence seemed to be stronger in the very early and in the early maturity class (Table 7). For example, the crosses involving Norland x TL 1859 and Catoosa x Norland had over 60.0 per cent of their progeny represented in the early classes. Several crosses involving late x late maturing parents had more of their progenies represented in the early class than in the late class. Krantz

(38) reported that most varieties were highly heterozygous for maturity and that maturity was controlled by many genes.

The progeny means of family lines tended to equal the means of their mid-parent values. The widest difference between progeny means and parents was found when two late maturing varieties were used as parents (Tables 3 and 7). Krantz (38) and Muller (46), in studying the inheritance of maturity, suggested that maturity of F_1 progenies lies within the maturity range of the two parents.

<u>Vigor of Clonal Generations Grown in Louisiana and North Dakota, 1963</u>

Table 8 shows the frequency distribution, mean, standard deviation, and coefficient of variability for vigor of progeny lines grown at Baton Rouge, Louisiana, and Grand Forks, North Dakota.

At both locations, Louisiana and North Dakota, parents expressed a range of very poor vigor to extreme vigor. Although environment affected vigor, heritable differences were found among parents grown in Louisiana and North Dakota.

In Louisiana, progeny means for vigor ranged from 1.48 to 3.02 units, standard deviation .640 to 1.281 units, and coefficient of variability 28.9 to 60.0 per cent. Figure 3 shows that 21.8, 25.4, 37.8, 13.3, and 1.8 per cent of clones from all ten progeny lines were in 1 (very poor) to 5 (extreme) vigor classes, respectively.

Segregation for vigor was evident for all progeny lines. Crosses involving Norland x TL 1859 and Catoosa x Norland produced 58.2 per cent and 52.8 per cent of their progeny in the very poor vigor class, respectively. The influence of Norland, which had poor vigor at

TABLE 8. Frequency distribution, mean, standard deviation, and coefficient of variability for vigor of the ten progeny lines grown in Louisiana and North Dakota during 1963

Pedigree number	Location	Distribution of clones in vigor classes[a] 1	2	3	4	5	Total clones	Mean	Std. dev.	% coef. var.
1	Louisiana	9	18	58	31	3	119	3.02	.895	29.6
	North Dakota	7	23	44	27	18	119	3.22	1.091	31.3
2	Louisiana	4	24	35	9	1	73	2.68	.774	28.9
	North Dakota	7	17	30	15	4	73	2.90	1.022	35.2
3	Louisiana	13	30	61	15	1	120	2.67	.858	32.1
	North Dakota	10	8	32	37	33	120	2.63	1.190	32.9
4	Louisiana	8	23	27	7	0	65	2.50	.843	33.7
	North Dakota	1	9	16	24	15	65	3.66	1.027	28.1
6	Louisiana	6	1	5	0	1	13	2.15	1.281	60.0
	North Dakota	0	5	5	2	1	13	2.92	.954	32.7
7	Louisiana	11	23	22	9	3	68	2.59	1.044	40.3
	North Dakota	5	6	23	15	19	68	3.56	1.208	33.9
8	Louisiana	11	12	30	12	2	67	2.77	1.000	36.1
	North Dakota	2	7	18	21	19	67	3.71	1.098	29.5
9	Louisiana	29	18	26	12	2	87	2.39	1.120	46.8
	North Dakota	10	12	19	34	12	87	3.22	1.220	37.8
10	Louisiana	38	21	10	3	0	72	1.69	.862	51.0
	North Dakota	8	17	33	10	4	72	2.82	.938	33.2
11	Louisiana	32	18	5	0	0	55	1.48	.640	43.2
	North Dakota	1	11	30	9	4	55	3.00	.800	26.6
Mean	Louisiana							2.39	.932	40.2
	North Dakota							3.26	1.054	32.1

[a]1 = very poor vigor
2 = poor vigor
3 = medium vigor
4 = vigorous
5 = extreme vigor.

Baton Rouge, Louisiana, seemed to contribute to the poor vigor obtained in the progeny. Bounty and White Rose seemed to have a strong genetic influence for obtaining high vigor when clones were grown at Baton Rouge, Louisiana. In many cases, the mean progeny within a family line exceeded the mean of the two parental varieties by over 20.0 per cent (Tables 3 and 8).

In North Dakota, the mean vigor of the progeny lines ranged from 2.63 to 3.71 units, standard deviation .800 to 1.220 units, and coefficient of variability 26.6 to 37.8 per cent. Means for all ten progeny lines (Figure 3) of 1 (very poor) through 5 (extreme) vigor classifications were as follows: 6.9, 15.6, 33.8, 26.3, and 17.5 per cent. This indicated that the clones from progeny lines were more vigorous than similar clones grown in Louisiana. Table 8 shows the amount of segregation that occurred within family lines. As was the case with progeny grown in Louisiana, Norland was found to have the poorest combining ability for vigor, while White Rose and Bounty were found to have excellent combining ability (Table 8, Figure 8). Several progeny means within a family line also exceeded the mean of the two parents involved when grown in North Dakota.

<u>Tuber Shape of Second Clonal Generations Grown in Louisiana and North Dakota, 1963</u>

Table 9 shows frequency distribution, mean, standard deviation, and coefficient of variability for tuber shape of second-year clonal generations grown in Louisiana and North Dakota. Parent classifications for tuber shape are found in Table 2. Tuber shape was not determined by actual measurement but by subjective rating on a composite sample.

TABLE 9. Frequency distribution, mean, standard deviation, and coefficient of variability for tuber shape of the ten progeny lines grown in Louisiana and North Dakota during 1963

Pedigree number	Location	Distribution of clones in tuber shape classes[a] 1	2	3	4	5	6	7	Total clones	Mean	Std. dev.	% coef. var.
1	Louisiana	15	1	1	63	3	1	32	116	4.48	1.895	42.3
	North Dakota	5	1	9	60	12	4	25	116	4.60	1.540	33.5
2	Louisiana	38	1	1	31	0	0	2	73	2.47	1.639	66.4
	North Dakota	38	6	4	25	0	0	0	73	2.21	1.377	62.3
3	Louisiana	61	0	1	51	0	0	7	120	2.64	1.806	68.4
	North Dakota	28	5	5	73	7	0	2	120	3.28	1.415	43.1
4	Louisiana	8	0	0	22	0	0	35	65	5.24	2.100	40.1
	North Dakota	2	0	0	32	11	0	20	65	5.00	1.488	29.8
6	Louisiana	6	0	0	7	0	0	0	13	2.62	1.557	59.4
	North Dakota	5	0	1	7	0	0	0	13	2.77	1.480	53.4
7	Louisiana	44	0	0	22	0	0	2	68	2.18	1.641	75.3
	North Dakota	16	1	5	45	1	0	0	68	3.17	1.290	40.6
8	Louisiana	36	0	0	23	2	0	2	63	2.38	1.710	71.8
	North Dakota	25	2	5	30	1	0	0	63	2.66	1.430	53.7
9	Louisiana	15	0	1	53	0	0	8	77	3.71	1.618	43.6
	North Dakota	17	2	4	47	3	2	2	77	3.40	1.470	43.2
10	Louisiana	33	1	0	28	1	0	5	68	2.75	1.881	68.4
	North Dakota	8	0	2	52	2	0	4	68	3.82	1.271	33.2
11	Louisiana	18	0	0	28	0	0	4	50	3.16	1.804	57.0
	North Dakota	3	2	5	25	6	2	7	50	4.26	1.507	35.3
Mean	Louisiana									3.16	1.765	59.3
	North Dakota									3.52	1.427	42.8

[a]1 = round
2 = round-oblong
3 = oblong-round
4 = oblong
5 = oblong-long
6 = long-oblong
7 = long.

Parental varieties used in this study ranged from round tuber types like the La Chipper and Irish Cobbler varieties to long tuber type like the variety White Rose. Some differences in tuber shape were found when parents were grown in Louisiana and North Dakota but, for the most part, a variety that was round or long at one location was similar at the other location. The greatest difficulty occurred when determining whether a parent was oblong or oblong-round or round-oblong. This was also true for classifying its progenies.

When second-year clonal generation families were grown in Louisiana, means of progeny lines ranged from 2.18 to 5.24 units. When similar clones were grown in North Dakota, the range of means within family lines were 2.21 to 5.00 units. The same progeny line at both locations produced the maximum numerical rating needed in establishing this range. Standard deviations were likewise quite similar at both locations ranging from 1.557 to 2.100 units in Louisiana to 1.271 to 1.540 units in North Dakota.

Coefficient of variability was high at both locations, ranging from 40.1 to 75.3 per cent in Louisiana to 29.8 to 62.3 per cent in North Dakota. This relative measure of variability expressed in per cent indicated that undesirable environment variation was manifested by the individual progenies within a family line. In addition to environment, the subjective method for determining tuber shape undoubtedly contributed to the amount of variability. This amount of variability in clonal material suggests a much improved experimental design and rating scale would be necessary if significant differences in progeny variabilities are to be detected.

Tuber Eye Depth of Second Clonal Generations

Grown in Louisiana and North Dakota, 1963

Table 10 shows the frequency distribution, mean, standard deviation, and coefficient of variability for eye depth of clones grown in Louisiana and North Dakota. Parental ratings are found in Table 2.

Parental varieties grown at both locations expressed a range of deep to shallow eyes. Parents used in this study afforded all combinations except deep x deep and very shallow x very shallow. Environmental conditions caused the eyes of parents grown in North Dakota to be slightly deeper than similar varieties grown in Louisiana (Table 2). Miller and McGoldrick (45) reported that potato varieties grown under long days had deeper eyes than the same varieties grown under short days. North Dakota growing seasons have an additional 2-4 hours more daylight per day than the spring season in Louisiana.

In Louisiana, the progeny mean for eye depth ranged from 3.15 to 3.92 units, standard deviation from .278 to .891 units, and coefficient of variability 7.0 to 28.2 per cent (Table 10). In North Dakota, the progeny mean ranged from 2.40 to 3.28 units, standard deviation .494 to .863 units, and coefficient of variability 16.9 to 34.7 per cent. The wide range in coefficient of variability indicated that the degree of variability within family lines was either quite small or relatively large depending on the parents used in certain crosses. A high coefficient of variability was found when Early Gem, La Chipper, and Irish Cobbler were used as parents.

In North Dakota, the coefficient of variability from these crosses ranged from 16.9 to 34.7 per cent. These parental recombinations

TABLE 10. Frequency distribution, mean, standard deviation, and coefficient of variability for tuber eye depth of the ten progeny lines grown in Louisiana and North Dakota during 1963

Pedigree number	Location	Distribution of clones in eye depth classes[a]					Total clones	Mean	Std. dev.	% coef. var.
		1	2	3	4	5				
1	Louisiana	0	10	21	79	6	116	3.69	.697	18.8
	North Dakota	4	21	52	38	1	116	3.09	.815	26.3
2	Louisiana	1	4	25	39	4	73	3.55	.759	21.3
	North Dakota	6	24	36	6	1	73	2.61	.805	30.8
3	Louisiana	7	18	46	48	1	120	3.15	.891	28.2
	North Dakota	14	55	40	11	0	120	2.40	.810	33.7
4	Louisiana	1	3	15	44	2	65	3.66	.686	18.7
	North Dakota	6	11	33	14	1	65	2.48	.863	34.7
6	Louisiana	0	0	2	11	0	13	3.92	.278	7.0
	North Dakota	0	2	9	2	0	13	2.92	.494	16.9
7	Louisiana	0	6	31	31	0	68	3.36	.643	19.1
	North Dakota	0	6	41	21	0	68	3.19	.583	18.2
8	Louisiana	0	9	23	31	0	63	3.37	.701	20.8
	North Dakota	0	9	45	9	0	63	3.00	.539	17.9
9	Louisiana	0	5	23	47	2	77	3.58	.652	18.2
	North Dakota	0	10	42	25	0	77	3.19	.645	20.2
10	Louisiana	0	7	28	33	0	68	3.38	.665	19.6
	North Dakota	0	17	39	12	0	68	2.93	.649	22.1
11	Louisiana	1	6	24	19	0	50	3.22	.729	22.6
	North Dakota	2	5	20	23	0	50	3.28	.801	24.4
Mean	Louisiana							3.49	.670	19.4
	North Dakota							2.90	.700	24.5

[a]1 = very deep
2 = deep
3 = medium
4 = shallow
5 = very shallow.

involved parents of wide differences in eye depth and resulted in a higher degree of heterozygosity within progeny lines. When progeny from crosses involving parents of either medium or shallow eyes were studied, such as Bounty crossed with ND 4524-16R, ND 4524-7R, or Viking, a relatively low and similar coefficient of variability existed at both locations.

Progeny means involving all ten clonal lines grown in Louisiana averaged from 1 (deep eyed) through 5 (very shallow eyed) as follows: 1.4, 9.5, 33.3, 53.6, and 2.1 per cent (Figure 4). Similar clones grown in North Dakota averaged from 1 (deep eyed) through 5 (very shallow eyed) as follows: 4.5, 22.4, 50.0, 22.6, and .4 per cent (Figure 4). This indicated that progeny lines grown in North Dakota produced clones which had deeper eyes.

When comparing the value of parental varieties, Irish Cobbler produced the largest population with very deep to deep eyes. This was quite evident when comparisons were made between the progeny means of Katahdin crossed with Early Gem, La Chipper, Irish Cobbler, and White Rose. Gene influence for deep eyes was also noted for the parental variety La Chipper (Table 10 and Figure 9).

Tuber Appearance of First-Year Clonal Generation Grown in North Dakota, 1962

Data on tuber appearance were recorded on all clonal lines saved for this study. A composite rating was used involving several aspects of tuber appearance. Good to excellent clones had tubers of uniform size and shape, free of growth cracks, heat sprouts, and second growth. Average clones possessed neither marked defects nor striking attributes.

Poor and very poor clones possessed definite undesirable traits in varying degrees.

Table 11 gives the frequency distribution, mean, standard deviation, and coefficient of variability for tuber appearance of first-year clonal generation grown in North Dakota. Means of progeny lines ranged from 2.97 to 3.34 units, standard deviation from .439 to .900 units, and coefficient of variability 13.5 to 28.0 per cent. Although coefficient of variability was higher than that for specific gravity in North Dakota in 1962, it still was considered comparatively low.

In this test little differences were found between the means of the progeny lines (Table 11). The majority of all clones were rated as medium or good in appearance. Crosses with the variety Norland showed the highest amount of segregation for tuber appearance. This was substantiated by the comparatively high standard deviation occurring in Pedigree Nos. 10 and 11 which had Norland as one of their parents (Table 11).

Tuber Appearance of Second Clonal Generation Grown in Louisiana and North Dakota, 1963

Table 12 shows the frequency distribution, mean, standard deviation, and coefficient of variability for tuber appearance of second clonal generations grown in Louisiana and North Dakota. Data concerning parental ratings are found in Table 2. Tuber appearance was rated in a similar manner as that of the first clonal generation grown in North Dakota in 1962.

TABLE 11. Frequency distribution, mean, standard deviation, and coefficient of variability for tuber appearance of the ten progeny lines grown in North Dakota during 1962

Pedigree number	Distribution of clones in appearance classes[a] 1	2	3	4	5	Total clones	Mean	Std. dev.	% coef. var.
1	2	16	64	32	2	116	3.13	.737	23.5
2	0	1	55	17	1	74	3.23	.483	14.9
3	0	5	73	39	3	120	3.33	.596	17.8
4	1	10	38	16	0	65	3.06	.676	22.0
6	0	0	10	3	0	13	3.23	.439	13.5
7	0	10	46	12	0	68	3.04	.562	18.4
8	0	7	30	25	2	64	3.34	.717	21.4
9	1	14	48	14	0	77	2.97	.644	21.6
10	2	14	22	28	2	68	3.21	.900	28.0
11	0	17	18	14	1	50	2.98	.826	28.0
Mean							3.15	.658	20.9

[a]1 = very poor appearance
2 = poor appearance
3 = medium appearance
4 = good appearance
5 = excellent appearance.

TABLE 12. Frequency distribution, mean, standard deviation, and coefficient of variability for tuber appearance of the ten progeny lines grown in Louisiana and North Dakota in 1963

Pedigree number	Location	Distribution of clones in appearance classes[a]					Total clones	Mean	Std. dev.	% coef. var.
		1	2	3	4	5				
1	Louisiana	14	31	41	27	3	116	2.79	1.021	36.6
	North Dakota	7	36	49	23	1	116	2.81	.879	31.2
2	Louisiana	4	7	38	24	1	74	3.17	.783	24.6
	North Dakota	1	11	42	19	1	74	3.10	.713	23.0
3	Louisiana	6	17	59	36	2	120	3.09	.837	27.0
	North Dakota	8	15	55	41	1	120	3.10	.870	28.0
4	Louisiana	10	16	34	5	0	65	2.52	.843	33.4
	North Dakota	19	25	19	2	0	65	2.06	.839	40.7
6	Louisiana	0	3	8	2	0	13	3.08	.641	20.8
	North Dakota	0	0	12	1	0	13	2.92	.277	21.9
7	Louisiana	2	7	41	18	0	68	3.10	.699	22.5
	North Dakota	2	4	25	36	1	68	3.44	.761	22.1
8	Louisiana	5	6	32	20	1	64	3.13	.851	27.1
	North Dakota	1	6	21	33	3	64	3.50	.777	22.2
9	Louisiana	2	10	36	27	1	77	3.19	.774	24.2
	North Dakota	0	2	35	36	4	77	3.54	.635	17.9
10	Louisiana	5	8	47	8	0	68	2.85	.713	25.0
	North Dakota	6	16	37	9	0	68	2.72	.802	29.4
11	Louisiana	3	8	32	6	1	50	2.88	.765	26.5
	North Dakota	3	14	15	17	1	50	2.98	.969	32.5
Mean	Louisiana							2.98	.793	26.8
	North Dakota							3.02	.752	26.9

[a]1 = very poor appearance
2 = poor appearance
3 = medium appearance
4 = good appearance
5 = excellent appearance.

For the most part, parents used in this study were well established varieties and had previously exhibited good tuber type in either Louisiana or North Dakota. In North Dakota, the varieties Catoosa, Irish Cobbler, White Rose, and TL 1859 were found to be the poorest in tuber appearance. In Louisiana, little differences were noted among parental varieties. Parental varieties were available to compare progenies from all crosses except poor x poor and excellent x excellent appearance.

The progeny means for tuber appearance in Louisiana ranged from 2.52 to 3.19 units, standard deviation .641 to 1.021 units, and coefficient of variability 20.8 to 36.6 per cent. In North Dakota, progeny means for tuber appearance ranged from 2.06 to 3.54 units, standard deviation .277 to .969 units, and coefficient of variability 17.9 to 40.7 per cent. When all ten families grown at both locations were compared, there was little difference in the average of progeny means, standard deviations, and coefficients of variability (Table 12). The effect of location on tuber appearance of all ten progeny lines grown in Louisiana and North Dakota during 1963 are shown in Figure 5. In some cases, a clone having a good appearance at one location would likewise have a good appearance at the other location. However, this was not the rule. Environment, in addition to genetics, also influenced clonal appearance. Heritability studies further substantiated this observation and will be discussed under heritability.

Certain parental recombinations were more useful in breeding for good tuber appearance. Table 12 shows that the parental recombinations found in Pedigree Nos. 1 and 4 produced progeny with the poorest appearance at both locations. This would indicate that the varieties Early Gem and White Rose had poor combining ability for tuber appearance. Conversely, the variety Bounty possessed good combining ability when used as a parent.

Correlation Coefficients

Correlation Coefficient and Association of Progenies Grown in North Dakota, 1962-1963, and Louisiana, 1963

Correlation coefficients for specific gravity of first clonal generations grown in North Dakota in 1962 and second clonal generations grown in Louisiana and North Dakota in 1963 equalled +.4084 and +.3392, respectively (Table 13). Correlation of specific gravity between second clonal generations grown in Louisiana and North Dakota in 1963 equalled +.3451 (Table 13). The pooled correlation coefficient would be significant for all generations and all locations; however, the correlation coefficient of certain progeny grown in Louisiana and North Dakota in 1963 was not statistically significant. The effect of environment seemed to be greatest in this particular test. According to Stevenson et al. (70), there are genetic differences among varieties and seedlings in their ability to produce a high specific gravity, but differences due to environment are often greater than the genetic or varietal differences.

Differences were evident between progeny lines grown in Louisiana and North Dakota when different parents were studied (Table 14). Several families showed a highly significant correlation coefficient, while others showed little or no correlation. Crosses involving White Rose and ND 4524-7R, two relatively low specific gravity parents, showed the poorest correlation. The high correlation existing between certain lines

TABLE 13. Pooled correlation coefficient and standard error of correlation coefficient of six characters from ten progeny lines grown in Louisiana and North Dakota during 1962 and 1963

Character	Correlation coefficient: Louisiana 1963 - North Dakota 1963	Correlation coefficient: Louisiana 1963 - North Dakota 1962	Correlation coefficient: North Dakota 1963 - North Dakota 1962
Specific gravity	+.3451** ± .0331	+.4084** ± .0313	+.3392** ± .0332
Plant maturity	+.4098** ± .0284		
Vigor	+.4174** ± .0364		
Tuber shape	+.4937** ± .0283	+.4387** ± .0303	+.4965** ± .0283
Tuber eye depth	+.3630** ± .0375	+.2127** ± .0332	+.3775** ± .0322
Tuber appearance	+.2999** ± .0371	+.1115* ± .0365	+.1678** ± .0369

** .115 significant at the 1 per cent level.

* .089 significant at the 5 per cent level.

TABLE 14. Correlation coefficient and standard error of correlation coefficient for specific gravity from ten progeny lines grown in North Dakota and Louisiana during 1962 and 1963

Pedigree number	Correlation coefficient		
	Louisiana - North Dakota 1963 1963	Louisiana - North Dakota 1963 1962	North Dakota - North Dakota 1963 1962
1	+.3837** ± .0792	+.4287** ± .0758	+.4498** ± .0741
2	+.2416* ± .1102	+.3915** ± .0991	+.3158** ± .1054
3	+.3648** ± .0791	+.4516** ± .0727	+.3868** ± .0776
4	+.0186 ± .1223	+.4411** ± .1233	+.2751* ± .1147
6	+.5404** ± .1964	+.4286** ± .2264	+.3228** ± .2484
7	+.3986** ± .1129	+.2998* ± .1120	+.5031** ± .0919
8	+.1392 ± .1245	+.4123** ± .1054	+.1491 ± .1242
9	+.5221** ± .0829	+.5401** ± .0807	+.5294** ± .0820
10	+.1300 ± .1192	+.3772** ± .1040	+.4038** ± .1015
11	+.4005** ± .1187	+.4285** ± .1155	+.5415** ± .0998

** Significant at 1 per cent level.

* Significant at 5 per cent level.

using either Katahdin or Bounty as parents would indicate that they would be beneficial in attaining high specific gravity in either Louisiana or North Dakota, providing desirable recombinations were made.

Data from Table 15 showed a relatively high correlation between specific gravity and maturity when clones were grown in Louisiana. The opposite was found in association of specific gravity and maturity when clones were grown in North Dakota. In Louisiana, correlation coefficient for specific gravity and maturity equalled -.4010, while in North Dakota similar correlated characters equalled +.0412 (Tables 19 and 20). The relatively high negative correlation coefficient in Louisiana would indicate that early maturing clones produced the highest specific gravity. The only cross with no correlation was Pedigree No. 11, Catoosa x Norland. These were two early maturing, low specific gravity parents. The highest negative correlation coefficient, -.5525, was found when Bounty was crossed with Viking (Table 15).

Correlation coefficients between specific gravity and vigor equalled -.2062 for clones from all families grown in Louisiana and +.0384 for all clones grown in North Dakota. Negative correlations indicated the least vigorous clones produced the highest specific gravity. The pooled correlation of all families grown in Louisiana was significant. However, non-significant correlations were obtained for over half of the progeny lines. Only progeny lines involving crosses between Bounty x ND 4524-7R, Bounty x ND 4524-16R, Bounty x Viking, and Norland x TL 1859 showed a significant negative correlation. At least one of the parents in these progeny lines was highly vigorous (Table 16). Although two progeny lines grown in North Dakota showed some association between

TABLE 15. Correlation coefficient and standard error of correlation coefficient for specific gravity and early plant maturity of ten progeny lines grown in Louisiana and North Dakota, 1963

Pedigree number	Correlation coefficient	
	Louisiana, 1963	North Dakota, 1963
1	-.3985** ± .0781	-.0731 ± .0909
2	-.4335** ± .0950	-.1159 ± .1155
3	-.3867** ± .0776	-.0146 ± .0913
4	-.3579** ± .1240	-.0687 ± .1215
6	-.6677** ± .1537	+.0696 ± .2760
7	-.4940** ± .1035	+.0671 ± .1170
8	-.4356** ± .1029	-.0237 ± .1269
9	-.5525** ± .0792	-.0976 ± .1129
10	-.2107 ± .1159	-.2502* ± .1137
11	-.0638 ± .1408	+.0710 ± .1407

** Significant at 1 per cent level.

* Significant at 5 per cent level.

TABLE 16. Correlation coefficient and standard error of correlation coefficient for specific gravity and vigor of ten progeny lines grown in Louisiana and North Dakota in 1963

Pedigree number	Correlation coefficient	
	Louisiana, 1963	North Dakota, 1963
1	-.1101 ± .0917	-.1372 ± .0926
2	+.0975 ± .1159	+.0365 ± .1169
3	-.1279 ± .0898	+.0652 ± .0909
4	-.0101 ± .1225	+.2809* ± .1239
6	-.2066 ± .2655	+.4433 ± .2229
7	-.3046** ± .1223	-.0926 ± .1112
8	-.4217** ± .1044	-.0200 ± .1269
9	-.3911** ± .0965	-.0925 ± .1130
10	-.3560** ± .1059	+.3010* ± .1103
11	-.1887 ± .1364	+.1420 ± .1386

** Significant at 1 per cent level.

* Significant at 5 per cent level.

specific gravity and vigor, the pooled correlation coefficient of all families almost equalled zero.

Data in Table 13 shows a correlation coefficient of +.4908 for maturity of second clonal generations grown in Louisiana and North Dakota. This indicated that if clones were late in North Dakota they were relatively late in Louisiana. Progeny lines had a range of correlation coefficient of +.3513 for Pedigree No. 7 to +.5264 for Pedigree No. 8 (Table 17). Bounty was the female parent in both of these crosses, while ND 4524-16R and ND 4524-7R, two related selections, were the males.

Vigor was also positively correlated for second-year clonal generations grown in Louisiana and North Dakota. A +.4174 correlation coefficient was obtained for this character (Table 13). Pedigree No. 3, Irish Cobbler x Katahdin, with a +.5659 and Pedigree No. 11, Norland x Catoosa, with +.2344 showed the highest and lowest correlation coefficient for vigor of progeny lines grown at the two locations (Table 17).

Correlation coefficients for the association of vigor and maturity are presented in Tables 19 and 20. The correlation coefficients for these two characters were +.5133 for clones grown in Louisiana and +.5318 for clones grown in North Dakota. These data show a close association of maturity and vigor. A positive correlation indicates that the most vigorous clones were the latest in maturity.

Data in Table 13 show the correlation coefficient for tuber shape, eye depth, and tuber appearance when clones were grown in Louisiana and North Dakota. Correlation coefficient for tuber shape equalled +.4937 (Table 13), indicating the close association and homogeneity for tuber shape when clones are grown at the two locations. The characters eye depth and tuber appearance showed a correlation coefficient of +.3630 and +.2999, respectively, for all families (Table 13). A positive correlation was also found for these characters when they were tested as first clonal generation in North Dakota and second clonal generation in Louisiana and North Dakota.

Eye depth was more highly correlated for second generation clones grown in Louisiana and North Dakota when deep-eyed parents such as Irish Cobbler and La Chipper were used (Table 18). Crosses between two relatively shallow-eyed parents showed little or no correlation.

Results from the computations of correlation coefficients for tuber appearance indicated that a few family lines were significant when grown in Louisiana and North Dakota. However, none were of significant magnitude to be of any real value from a predictive standpoint. Clonal lines having Katahdin as a parent seemed to show the greatest association (Table 18).

Correlation coefficients are used to measure the magnitude of linear relationships or the degree to which variables vary together. When linear relationship is small, the correlation coefficient is near zero. The association between individual variables or clones is important in determining whether a particular clone has the same or different character expression when grown under two sets of environmental conditions.

In this study, one of the main objectives was to determine whether a clone having high specific gravity in the North would likewise have a high specific gravity when grown in the South. Results from this study

TABLE 17. Correlation coefficient and standard error of correlation coefficient for plant maturity and vigor of ten progeny lines grown in Louisiana and North Dakota in 1963

Pedigree number	Correlation Coefficient — Character: Plant maturity	Correlation Coefficient — Character: Vigor
1	+.4944** ± .0702	+.3912** ± .0786
2	+.3960** ± .0986	+.4636** ± .0919
3	+.5121** ± .0673	+.5659** ± .0892
4	+.3639** ± .1219	+.2694* ± .1216
6	+.7750** ± .1109	+.1469 ± .2708
7	+.5264** ± .1176	+.4823** ± .1136
8	+.3513** ± .1113	+.3929** ± .1251
9	+.4858** ± .0871	+.4212** ± .1108
10	+.4650** ± .0950	+.3144** ± .1140
11	+.4122** ± .1174	+.2344* ± .1337

** Significant at 1 per cent level.

* Significant at 5 per cent level.

TABLE 18. Correlation coefficient and standard error of correlation coefficient for tuber eye depth and tuber appearance of ten progeny lines grown in Louisiana and North Dakota in 1963

Pedigree number	Correlation coefficient — Character: Tuber eye depth	Correlation coefficient — Character: Tuber appearance
1	+.3336** ± .0914	+.1002 ± .0919
2	+.5009** ± .1136	+.3087** ± .1059
3	+.4247** ± .0748	+.2966** ± .0833
4	+.2499* ± .1163	+.2372* ± .1171
6	+.0468 ± .2767	+.0361 ± .2769
7	+.3344** ± .1093	+.4248** ± .1009
8	+.2562* ± .1233	+.1705 ± .1233
9	+.2333* ± .1139	+.2859** ± .1047
10	+.4742** ± .1212	+.1083 ± .1198
11	+.3740** ± .1410	+.3473* ± .1244

** Significant at 1 per cent level.

* Significant at 5 per cent level.

TABLE 19. Correlation between Louisiana second clonal generation observations for specific gravity and plant maturity and fourteen other sets of observations

Correlated character	Second clonal generation, Baton Rouge, La. — Correlation coefficient — Character: Specific gravity	Plant maturity
First clonal generation Grand Forks, North Dakota		
Specific gravity	+.4084	-.3411
Tuber eye depth	-.0687	+.0032
Tuber shape	-.0826	+.0300
Tuber appearance	+.5105	-.0062
Second clonal generation Grand Forks, North Dakota		
Specific gravity	+.3451	-.0745
Plant maturity	-.2401	+.4908
Vigor	-.1426	+.2981
Tuber eye depth	-.0689	+.0257
Tuber shape	-.0393	-.0248
Tuber appearance	+.1106	-.0903
Second clonal generation Baton Rouge, Louisiana		
Specific gravity	1.0000	-.4010
Plant maturity	-.4010	1.0000
Vigor	-.2062	+.5133
Tuber eye depth	-.0755	+.0083
Tuber shape	-.1702	+.1176
Tuber appearance	+.2667	-.2620

TABLE 20. Correlation between North Dakota second clonal generation observations for specific gravity and plant maturity and fourteen other sets of observations

Correlated character	Second clonal generation, Grand Forks, N.Dak. Correlation coefficient Character	
	Specific gravity	Plant maturity
First clonal generation Grand Forks, North Dakota		
Specific gravity	+.3392	-.4155
Tuber eye depth	-.0110	+.0096
Tuber shape	-.1717	+.1137
Tuber appearance	+.0955	-.0827
Second clonal generation Grand Forks, North Dakota		
Specific gravity	1.0000	+.0412
Plant maturity	+.0412	1.0000
Vigor	+.0384	+.5318
Tuber eye depth	+.0081	-.1039
Tuber shape	-.1103	-.0064
Tuber appearance	+.2358	-.2052
Second clonal generation Baton Rouge, Louisiana		
Specific gravity	+.3451	-.2401
Plant maturity	-.0745	+.4908
Vigor	+.0182	+.4067
Tuber eye depth	+.0057	-.0181
Tuber shape	+.0851	+.1063
Tuber appearance	+.1343	-.1711

and from other investigators have shown that environment greatly affects specific gravity. The amount of variability found between certain varieties grown on the same farm has been well illustrated by Stevenson and Whitman (72). Figure 6 shows that some clones within a progeny had some degree of stability and would produce a relatively high degree of specific gravity when grown in either Louisiana or North Dakota. When determining the number of clones with a specific gravity exceeding 1.084 in North Dakota, there was a range of 4.8 per cent to 35.6 per cent between progeny lines (Figure 6).

The lower limits of clones having a specific gravity of 1.064 and 1.084 would not be considered exceptionally high. However, many clones exceeded these lower limits by several increments in specific gravity. These lower limits were also the same as or exceeded the mean of both parents grown at a particular location. Gene influence of parents used in this study was important in obtaining clones with a high specific gravity. In most cases, crosses involving parents of high specific gravity gave the highest per cent of clones that had a high specific gravity at both locations (Figure 6). Crosses of low x low, low x medium, and low x high produced progeny of the lowest specific gravity when grown in either Louisiana or North Dakota. Association between first clonal generations grown in North Dakota in 1962 and second clonal generations in North Dakota and Louisiana showed an even greater number of clones with low specific gravity at one or more of the locations. However, it was difficult to consider the lower limits in specific gravity of clones grown as first clonal generation in North Dakota in 1962. Several investigators (12) have reported that certain factors, such as seedling size, affect the efficiency of selecting in the first clonal generation.

Figures 7, 8, 9 and 10 show the per cent of clones from different progeny lines that expressed desirable character expression for four characters when grown in Louisiana and North Dakota, and also the per cent of clones that were desirable when grown at both locations. Character expression was found to vary for each character and for each parental recombination.

Heritability

Heritability in the broad sense for five characters, or the ratio of total genetic variance to phenotypic variance, was estimated for all clones grown as second clonal generation in Louisiana and North Dakota.

Heritability is used in both a broad sense and a narrow sense. However, due to inadequacies in the crossing of parents, additive genetic variance was not estimated. Therefore, heritability in the narrow sense --additive genetic variance/phenotypic variance--was not calculated.

According to Hanson (29), heritability in the broad sense considers the total genetic variability in relation to the phenotypic variability. The genotype is considered as the unit in relation to the environment. Heritability in the narrow sense considers only the additive portion of the genetic variability in relation to the phenotypic variability. Several investigators (30; 36) have reported on heritability in the broad sense based on single plants, single plots, replicated plots, and on samples of plots to describe genetic variability in quantitative plant genetics.

Hanson et al. (30) further point out that in asexually propagated crops any combination of genetic factors which yields superior genotypes can be utilized through clonal propagation. Heritability in a broad sense would then have a meaning for asexually reproduced plants since all genetic variability is useable.

Total variance was separated into three sources--location, clone or genotype, and clone by location interaction. Hanson et al. (30) discussed the use of a formula for heritability in which interaction components are not divided by the number of locations, years, or replications involved. According to these writers, this is a more appropriate method when comparing heritability estimates for different characters and different environments and experiments. This method was referred to as heritability of a single plot. The following formula was used for estimating heritability:

$$\frac{\sigma^2 \text{ clones}}{\sigma^2 \text{ clones} + \sigma^2 \text{ clones x location}} \times 100 = \text{heritability estimate for single plot}$$

Heritability in the Broad Sense

Heritability estimates for specific gravity ranged from 1.5 to 50.1 per cent (Table 21). Heritability estimates were similar for all crosses involving Early Gem x Katahdin, La Chipper x Katahdin, and Irish Cobbler x Katahdin, but was of a very low magnitude when White Rose was crossed with Katahdin. Crosses involving Bounty x ND 4524-16R and Bounty x Viking were also quite similar, but Bounty x ND 4524-7R was found to be comparatively low. The parents Bounty, ND 4524-16R, and Viking all produced progeny with relatively high specific gravity, while ND 4524-7R produced progeny with very low specific gravity. Apparently

TABLE 21. Heritability on a single-plot basis for five characters grown as second-year clonal generation in Louisiana and North Dakota in 1963

Pedigree number	Per cent heritability, Character: Specific gravity	Plant maturity	Vigor	Tuber eye depth	Tuber appearance
1	34.3	49.3	38.4	33.1	9.9
2	23.8	39.1	44.6	50.1	30.8
3	33.4	50.3	53.7	42.4	30.0
4	1.5	36.4	30.9	24.4	23.8
7	39.6	52.6	47.8	33.4	42.4
8	13.3	35.0	38.9	25.0	18.3
9	50.1	48.7	42.1	22.4	28.2
10	12.3	45.5	30.9	47.7	11.1
11	32.8	40.5	23.0	37.2	33.8
Mean	26.7	44.2	38.9	35.1	25.4
Range	1.5-50.1	35.0-52.6	23.0-53.7	22.4-50.1	9.9-42.4

a greater percentage of the variance was genetic in the crosses involving Early Gem x Katahdin, La Chipper x Katahdin, Irish Cobbler x Katahdin, Bounty x ND 4524-16R, and Bounty x Viking than Katahdin x White Rose and Bounty x ND 4524-7R. A comparatively high estimate of heritability was also found for the cross Catoosa x Norland, but a low estimate was found for Norland x TL 1859.

Heritability estimates for maturity were quite high for all progenies. The magnitude of the estimates for all crosses except White Rose x Katahdin indicated that a higher proportion of the phenotypic variance resulted from genetic effect. Heritability for crosses ranged from 35.0 to 52.6 per cent (Table 21). Lowest heritability estimates were found for the crosses White Rose x Katahdin and Bounty x ND 4524-7R.

The heritability estimates for plant vigor were also quite high except for the cross involving Catoosa x Norland which was somewhat low. Heritability estimates for all crosses ranged from 23.0 to 53.7 per cent (Table 21).

Heritability estimates for eye depth ranged from 22.4 to 50.1 per cent for all crosses involved in this study. The crosses involving Katahdin x White Rose and Bounty x Viking expressed the lowest heritability estimates, while all other crosses expressed relatively high heritability estimates (Table 21).

When all characters were compared, heritability estimates for tuber appearance showed the least amount of continuity. The range in heritability for all crosses was 9.9 to 42.4 per cent (Table 21). Consequently, the estimation of heritability in the broad sense of several crosses was of a magnitude to indicate that very little genetic variance was present in the phenotypic variance. No doubt the subjective nature of the test for tuber appearance also contributed to the low estimate of heritability of certain crosses.

Estimates of heritability for the crosses Early Gem x Katahdin, La Chipper x Katahdin, Irish Cobbler x Katahdin, and White Rose x Katahdin indicated the presence of some genetic variance for Katahdin x La Chipper and Katahdin x Irish Cobbler, but very little for Early Gem x Katahdin and White Rose x Katahdin. When comparing the crosses involving Bounty, the lowest heritability estimate was found with Bounty x ND 4524-7R. Norland x TL 1859 also expressed low heritability estimates. Mullins (47) found single-plot heritability estimates for several progenies and clones to be 21.1 per cent for tuber appearance when plots were grown in Minnesota and North Dakota.

In general, results of heritability estimates for tuber appearance would be too inconsistent to effectively select for tuber appearance in Louisiana and North Dakota. However, if some basis for the reliability of estimates of heritability for tuber appearance can be made certain, parents would have more genetic and less environmental variance. For example, the cross between Bounty and ND 4524-16R had a heritability estimate of 42.4 per cent. Both of these parents have good to excellent tuber appearance.

Heritability estimates for specific gravity and tuber appearance of first generation clones grown in North Dakota and second generation clones grown in both Louisiana and North Dakota were compared. Heritability estimates for specific gravity were very similar for all progenies except the cross Bounty x ND 4524-7R and Bounty x ND 4524-16R

(Table 22). Considering the same clonal generations grown in Louisiana and North Dakota, heritability estimates for tuber appearance showed little or no continuity (Table 22). Heritability estimates for crosses of first and second clonal generations grown in North Dakota ranged from 14.7 to 54.2 per cent for specific gravity and zero to 36.1 per cent for tuber appearance.

Genetic Advance Expected from Selection

The rate of genetic advance under selection is influenced by several factors including the magnitude of differences in genetic variability of the original population, the amount of environmental influence exerted upon the genetic effects, and the intensity of selection pressure.

One of the important factors associated with heritability estimates is the use of these estimates in computing the amount of observed variability which may be expected and retained from one generation to the next and from location to location. Such a test is possible when progeny are grown from a generation or location for which heritability estimates have been computed. Plaisted (53) used heritability estimates of components of variance to obtain comparative measures of average genetic advance which could be expected under different combinations of varieties, seasons, locations, and replications in experiments to evaluate specific gravity. Combined analyses were made of specific gravity data obtained from several locations in the northern part of the United States. He obtained genetic advances ranging from 2.5 to 7.5 (coded by .001) units of specific gravity when one, two, and four replications were compared to several locations and years.

TABLE 22. Heritability on a single-plot basis for specific gravity and tuber appearance of clonal generations grown in Louisiana and North Dakota

Pedigree number	Per cent heritability: 1st clonal generation N. Dak., 1962 - 2nd clonal generation La., 1963 — Character: Specific gravity	Tuber appearance	1st clonal generation N. Dak., 1962 - 2nd clonal generation N. Dak., 1963 — Character: Specific gravity	Tuber appearance
1	41.3	14.3	44.1	0
2	37.9	0	31.5	.5
3	41.7	16.4	38.7	36.0
4	7.3	7.7	24.1	25.8
7	29.7	9.8	50.3	0
8	40.8	7.9	14.7	23.7
9	52.8	9.0	52.8	13.3
10	38.3	0	40.3	36.1
11	35.0	33.8	54.2	26.8
Mean	36.1	10.9	39.0	23.8
Range	7.3-52.8	0-33.8	14.7-54.2	0-36.1

The use of such estimates to predict selection advance in the next clonal generation can be helpful in determining appropriate selection procedures. Allard et al. (3) have used heritability estimates in which the components are divided by the number of locations, years, or replications involved. In this test, total variance was separated into sources, locations, clone or genotype, and clone by location interactions. The estimated variance components were obtained from the same source as heritability estimates for single plots.

Clonal heritability, used to predict selection advance from second to third clonal generation, was estimated as:

$$\frac{\sigma^2 \text{ clone}}{\sigma^2 \text{ clone} \quad \frac{\sigma^2 \text{ clone x location}}{2}} = \text{clonal heritability estimates}$$

From the heritability estimates, expected genetic advance in the next generation was calculated as GS = (K) (σA) (H)

where:

GS = Expected genetic advance under selection.

(K) = Selection differential expressed in units of standard deviation assuming normal distribution of observation. According to Allard (3), for 10.0 per cent selection, this is 1.76.

(σA) = Phenotypic standard deviation.

(H) = Heritability.

GS = K x σA x H

$$\text{Per cent gain} = \frac{\text{GS}}{\text{Mean for character at two locations}}$$

Tables 23 and 24 show the predicted selection advance from the second to the third clonal generation for several characters. The predicted advance from the second to third clonal generation is based on the assumption that the top 10.0 per cent of the clones are selected.

Expected Selection Advance in Next Clonal Generation

The expected gain in specific gravity (Table 23) ranged from .022 to 5.855 (.001) units of specific gravity or, expressed in terms of population means, a range of .03 to 7.9 per cent advance. These predicted advances in specific gravity were comparable to those found by Plaisted (53). Plaisted (53) designed a table which could be used as an aid in evaluating gains for specific gravity. His table showed that expected genetic advance was 6.616 (.001) units of specific gravity for thirty varieties grown for two years at four locations in one replication. As shown in Table 23, the crosses Early Gem x Katahdin, La Chipper x Katahdin, and Irish Cobbler x Katahdin had a higher per cent selection advance than White Rose x Katahdin. The crosses Bounty x ND 4524-16R and Bounty x Viking likewise had a higher per cent selection advance than Bounty x ND 4524-7R.

The expected selection advance for plant maturity and vigor are also shown in Table 23. By assuming the selection of the top 10.0 per cent for plant maturity, the selection advances ranged from .732 to 1.170 units of maturity or, expressed in terms of population mean, a range of 25.5 to 43.9 per cent selection advance. The cross White Rose x Katahdin gave the lowest per cent selection advance for plant maturity. Per cent selection advance for other progenies were quite similar; however, several of the progenies involving very early x early or early x

TABLE 23. Clonal heritability and expected selection advance[a] for specific gravity, plant maturity, and vigor of second clonal generation lines grown in Louisiana and North Dakota

Pedigree number	Specific gravity			Plant maturity			Vigor		
	Per cent heritability	Unit gain[b]	Per cent advance	Per cent heritability	Unit gain	Per cent advance	Per cent heritability	Unit gain	Per cent advance
1	51.1	4.792	6.60	66.7	1.104	34.4	55.5	.815	26.0
2	38.5	3.084	4.10	56.1	.798	28.5	61.7	.844	30.2
3	48.8	3.977	5.20	66.9	1.086	37.8	69.9	1.123	35.7
4	2.9	.022	.03	53.3	.785	25.5	41.8	.554	17.8
7	56.8	5.331	7.10	68.9	1.117	38.7	64.6	1.125	36.5
8	23.5	2.094	3.00	51.9	.822	29.0	55.6	.870	26.9
9	66.8	5.855	7.90	65.5	1.170	43.0	59.1	1.035	36.8
10	21.8	1.667	2.30	62.5	.983	43.9	47.2	.611	27.0
11	49.4	3.416	4.80	57.7	.732	32.6	37.3	.377	16.9
Mean	40.0	3.359	4.60	61.1	.955	34.8	54.7	.817	28.2

[a]Assuming the top 10.0 per cent are selected. Selection advance is from the second to third clonal generation.

[b]Specific gravity coded by (.001).

TABLE 24. Clonal heritability and expected selection advance[a] for tuber eye depth and tuber appearance of second generation clonal lines grown in Louisiana and North Dakota

Pedigree number	Tuber eye depth			Tuber appearance		
	Per cent heritability	Unit gain	Per cent advance	Per cent heritability	Unit gain	Per cent advance
1	49.6	.543	16.0	18.1	.226	8.6
2	66.7	.802	26.0	47.0	.505	16.2
3	59.5	.756	27.2	45.7	.555	17.9
4	39.2	.429	14.0	38.4	.452	19.7
7	50.0	.445	13.6	59.4	.651	20.5
8	40.0	.352	11.0	31.9	.351	10.6
9	36.5	.328	9.7	43.9	.441	13.1
10	64.6	.646	24.0	7.1	.120	4.3
11	54.3	.613	18.9	50.5	.641	21.9
Mean	51.2	.546	17.4	38.0	.438	14.8

[a]Assuming the top 10.0 per cent are selected. Selection advance is from the second and third clonal generation.

medium had a higher per cent expected selection advance than crosses involving late x late or late x medium maturing parents.

Expected selection advance for vigor ranged from .377 to 1.125 units or, expressed in terms of population mean, a range of 16.9 to 36.8 per cent selection advance. The crosses White Rose x Katahdin and Catoosa x Norland had the lowest per cent selection advance. Progeny from other crosses involving Katahdin and progeny from Bounty showed a high per cent selection advance (Table 23).

The expected selection advance for shallow tuber eye depth and excellent tuber appearance are found in Table 24. Expected selection advance for tuber eye depth ranged from .328 to .802 units or, expressed in terms of population mean, a range of 9.7 to 27.2 per cent selection advance. When comparing the selection advance of the top 10.0 per cent of the clones for tuber eye depth, the crosses La Chipper x Katahdin and Cobbler x Katahdin had a higher per cent selection advance than Early Gem x Katahdin and White Rose x Katahdin. Both crosses involving the parent Norland were also relatively high.

Expected selection advance from the second to third generation for excellent tuber appearance ranged from .120 to .651 units or, expressed in terms of population mean, a range of 4.3 to 21.9 per cent selection advance (Table 24). Mullins (47) found an 11.1 per cent selection advance for tuber appearance when several clones were grown in Minnesota and North Dakota. The cross between Catoosa x Norland produced the lowest per cent selection advance, while Norland x TL 1859 produced the highest per cent selection advance when the 10.0 per cent of the top clones were selected. The cross Bounty x ND 4524-16R was twice as high in units gained and per cent selection advance as the cross Bounty x ND 4524-7R. ND 4524-16R and ND 4524-7R are sister selections. In crosses involving the parent Katahdin crossed with Early Gem, La Chipper, and Irish Cobbler, the progenies from La Chipper and Irish Cobbler were higher than Early Gem in units gained and per cent selection advance for good tuber appearance.

For many of these characters, a rather high estimated genetic selection advance was found. This was particularly true for plant maturity and vigor. Although vigor and plant maturity are influenced by environment, these characters would probably have a more stable expression from season to season. Results of specific gravity tests, which were direct measurements, agreed with other workers (47, 53). The most logical reason for the rather high estimates for some characters was the fact that the clones were tested only once at each of two locations. Therefore, not all of the variance attributed to clones is expected to be genetic. Plaisted (53) illustrated the effect of varying numbers of varieties, locations, and years on average genetic advance. He pointed out that, regardless of the efficiency figures in favor of single replication with more locations and years, the flexibility and ability of the data would be greater where there is more than one replication at a location. He further pointed out that more than one replication would more than repay the additional effort involved.

Heritability estimates and expected genetic advance have been reported for several other asexually produced crops. Keller and Likens (36) found expected gains to vary from 14.0 to 61.0 per cent for several characters associated with hops, <u>Humulus lupulus</u> L. Their data were computed on a single and replicated plot basis.

DISCUSSION

Research has shown that environment has a definite effect on the genetic behavior of certain characters found in the Irish potato. The forces of environment often interfere with the genetic expression of characters so as to produce a phenotype that is not necessarily indicative of the genotype. Stevenson et al. (70) state:

> If it were not for environmental effects or if all potatoes were grown under the same environment, it would be easy to name varieties most suitable for various methods of cooking, such as baking, boiling, chipping or french frying.

However, even though environment does have an effect on the expression of most characters, the release of new potato varieties with wider adaptation indicates that progress has been made in overcoming some degree of environmental effect. Allard (4) reports that plant breeders have long been aware that phenotype response to the change of environment is not the same for all genotypes and they generally accept the premise that the interplay between genotype and environment has its basis in the biochemistry and biophysics of development. However, numerous studies of development at the molecular and higher levels of organization have led to few basic principles which have been particularly beneficial to plant breeders (4).

Adaptation trials at the state and regional level have been conducted to study the response of certain varieties over a wide range of environmental conditions. These trials have been beneficial, but they have added little information regarding the heritability and association of certain characters.

According to Stevenson and Whitman (72), it is desirable from a plant breeding standpoint to know how much a clonal line will vary in quality and specific gravity when grown under conditions found in various potato-growing sections in the United States and to determine, if possible, whether some varieties are more resistant to environmental changes than others. If a widely adapted variety can be developed, the asexual nature of reproduction found in the potato would lead to perpetuating this variety with great precision. This can be a great advantage as any new recombinations of genetic factors which produce superior genotypes can be utilized through clonal propagation, irrespective of the amount of heterozygosity present.

Like most other crops, selection of superior clones in a genetically based population is the principal procedure used by all potato breeders, regardless of the breeding method used. Any breeding program is most efficient when selection and evaluation of progeny and parental material can be accomplished in early generations. To measure the efficiency of selection in an asexually propagated crop, statisticians have designed a method referred to as heritability in the broad sense or clonal repeatability (29, 30).

According to Hanson (29), the concept of heritability originated as an attempt to describe whether differences actually observed between individuals arose from the differences in genetic make-up between the individuals or resulted from different environmental forces. As a genetic parameter, heritability is a prediction of the breeding value based on phenotypic measurements. In asexually propagated crops, selection of superior genotypes for vegetative propagation in succeeding years can be based on the entire genetic make-up of an individual.

Favorable additive dominance or epistatic gene combinations can be selected and propagated. Heritability in the broad sense or the ratio of total genetic variation to total phenotypic variation can, therefore, be used as a measure of selection efficiency. If heritability estimates are high, this would suggest that considerable progress can be made by individual plant selection in early clonal generations. Knowledge of heritability for the characters in question obtained from progeny tested under wide environmental conditions would result in a substantial saving of time and money. If selection can be made efficiently, the elimination of undesirable parents can be made in early stages of the breeding program. Most breeding programs have a population limitation and the elimination of undesirable material will increase the chances of finding desirable clones. To completely separate the components of the ratio of total genetic variance to total phenotypic variance is probably not possible, although it is possible to estimate them within a certain limit of error.

Hanson (29) points out that heritability statements will depend upon the restrictions one wishes to make for the definition and the basis (reference unit) which one uses to determine a measure. For quantitative measure in plant breeding, a plant, a field plot, replicated field plot in one environment, or replicated field plots in two or more environments may be considered as the reference unit and each reference unit would affect the heritability statement made. He further points out that, while heritability on a single-plot basis has limited utility, heritability based on large samples of environments and plots within environments would also have limited utility, since heritability for any character can be made as close to 1.0 as desired by unlimited sampling. Heritability estimates for certain characters have been made on several asexually propagated crops (30; 36).

Estimating the selection advance for future clonal generations is also beneficial in evaluating the efficiency of a breeding program. Selection of superior genotypes for further asexual propagation and testing is based on phenotypic evaluation in early clonal generations. Since the selected individual itself is propagated in future clonal generations, favorable additive dominance and epistatic gene combinations contribute to the clonal value of the genotype. The expected clonal advance is, therefore, the product of the selection differential and an estimate of heritability in the broad sense. For a 10.0 per cent selection of the most desirable clones in a given population, selection differential has a value of 1.76 (3).

Nine cross-pollinations and one self-pollination representing 710 clones were used in the present study. All progeny lines except Pedigree No. 6, Katahdin selfed, had sufficient population size to make reliable statistical measurements. Heritability estimates were not made on the progeny line representing Katahdin selfed.

Climatological data collected for this study indicated that all clonal generations were grown under different environmental conditions. According to Comstock and Moll (20), environments are recognized as being either micro or macro environments. Their description of environments would infer that these tests were conducted under the extremes of a macro environment.

The 1962 season in North Dakota was marked by very wet weather at planting time and during the later part of the season. Temperatures were below normal early in the season but were fairly warm at harvest time. A somewhat different environment occurred in North Dakota during 1963 which had moderately high temperatures throughout most of the season and much below seasonal rainfall (7.03 inches). The spring season in Louisiana with only 7.74 inches of rain was recorded as one of the driest seasons on record. High temperatures prevailed in Louisiana during the later part of the season.

In the present study, the lower specific gravity of tubers from parental varieties and their progenies grown in the South was expected. Research has shown that when mean monthly temperatures exceed 70° F. the accumulation of carbohydrates in tubers is retarded, thus causing lower specific gravity (49). In addition, night temperature which did not go below 60° F. for four weeks prior to harvest encouraged high respiration so as to lower specific gravity.

In contrast to conditions in Louisiana, decreasing temperatures prior to harvest in North Dakota during the fall of 1963 resulted in higher specific gravity at this location. Talburt and Smith (74) have shown that cool temperatures late in the season result in potatoes with higher specific gravity than those produced at high temperatures. This again is the result of a smaller loss of carbohydrates by respiration when potatoes are grown at cooler temperatures. The high rainfall and low temperatures during most of the season were factors contributing to a somewhat lower specific gravity in North Dakota during 1962.

For the most part, second clonal generation progeny means were considered the most accurate measurements in this study. A correlation coefficient of +.3451 was found for specific gravity of second clonal generations grown in Louisiana and North Dakota. The correlation coefficients of +.4084 for first clonal generations grown in North Dakota and second clonal generations grown in Louisiana, and +.3392 for first clonal generations grown in North Dakota and second clonal generations grown in North Dakota showed that these generations were also positively correlated for specific gravity. Actually, there was very little difference between correlation coefficients of all three clonal tests; however, selection for specific gravity and other characters in the first clonal generation would be doubted by many. Several researchers are of the opinion that there are too many variables such as seedling tuber size, rest period, and seedling vigor that will affect either favorable or unfavorable character selection in the first generation.

In spite of these assumptions, data showed that some degree of reliability can be achieved for certain parental recombinations when selected in either the first or second clonal generation. It should be noted that it is the common practice for most potato breeders to evaluate and screen progeny for specific gravity and other characters in the first clonal generation.

Although correlation coefficients were not exceptionally high for any clonal generation, it was interesting to find that the highest correlation coefficient of all clonal tests was found for first clonal generations grown in North Dakota and second clonal generations grown in Louisiana. It would be reasonable to assume that the interaction of environment and hereditary factors was in closer proximity in these clonal generations, thus causing this association. Results from these correlation coefficients would indicate that the first clonal generation reading plus the second clonal generation reading for specific gravity would be sufficient to establish progeny values for this character.

The segregation in progenies from all varieties used as parents showed that they were highly heterozygous for the character specific gravity. Segregation was high for progenies grown at all locations; however, depending on the parents used, certain recombinations showed a higher degree of segregation. In most cases, the crosses between low x medium or low x high specific gravity parents produced the highest degree of segregation. Similar results were found by Akeley and Stevenson (2).

The cross of Bounty x ND 4524-16R showed what might be expected when two parents, both having high specific gravity, were crossed. Although other recombinations produced clones that were as high in specific gravity, this recombination produced a consistent number of clones that were high at both locations. The crosses La Chipper x Katahdin and Irish Cobbler x Katahdin, which represented a high x medium combination, also produced a fairly high number of clones that were high in specific gravity at both locations. The cross Bounty x ND 4524-7R showed the amount of segregation and genetic influence that might be expected when two varieties, one high and the other low in specific gravity, are crossed. In this particular cross, a high degree of segregation was evident; however, the majority of clones were low in specific gravity. Further evidence of genetic influence and segregation was found in the cross Catoosa x Norland, two low specific gravity parents, which produced the most clones represented in the low specific gravity class when grown at both locations.

Heritability in the broad sense for progeny grown as first clonal generations in North Dakota and second clonal generations in Louisiana and North Dakota was very beneficial in establishing selection efficiency and parental worth for specific gravity. Estimates of heritability for most all parental recombinations showed quite similar associations in each clonal test. Interaction of genotype with any environmental source of variance will reduce heritability estimates and selection advance. Of the four parents crossed with Katahdin, the variety White Rose showed a relatively low heritability in all three clonal tests. In most cases, progeny from the other combinations, Early Gem x Katahdin, La Chipper x Katahdin, and Irish Cobbler x Katahdin, produced heritability estimates that were quite high and uniform in all clonal tests. Progeny from other parental recombinations grown in the three clonal tests showed similar heritability estimates, except the crosses Bounty x ND 4524-16R and Bounty x ND 4524-7R.

One of the most important factors associated with heritability was that when certain parents were used they were very specific in transmitting heritable characters. High specific gravity parents generally produced the highest heritability estimates, indicating that a greater percentage of variance was genetically controlled and a lesser percentage was controlled by environment. The best examples were the crosses involving Bounty x ND 4524-16R, Bounty x ND 4524-7R, and Bounty x Viking. The highest heritability estimates were found when Bounty was crossed with the two high specific gravity parents, ND 4524-16R and Viking.

The expected genetic selection advance in the next generation predicts the phenotypic superiority of the selected portion of the population. The expected genetic selection advance for specific gravity indicated that if high specific gravity parents were used, a high per cent selection advance was obtained.

Under these circumstances, it would seem logical to use only parents with high specific gravity if one expects to develop varieties that are high in specific gravity in both Louisiana and North Dakota. When high specific gravity is the criterion, the potato breeder should attempt to use cycle phenotypic recurrent selection designed by Plaisted and Peterson (54). It would be quite obvious that parent varieties like White Rose and ND 4524-7R would be excluded from this type of a program.

Although heritability estimates and selection advance were greater when both parents had high specific gravity, certain parents representing low x medium and high x medium also had fairly high estimates of heritability and selection advance. Genetic make-up of such recombinations was such that progeny from these crosses was less affected by the forces of environment. Heritability estimates in the broad sense merely indicate the relation of variance due to phenotype to the total genetic variance. If the percentage is large, the character is highly heritable; if it is small, environment is correspondingly prominent in character expression.

Results from the data concerning specific gravity showed that there were differences among progeny that reflected superiority of parental recombinations. The higher heritability estimates were substantiated by the higher correlation coefficients for specific gravity of certain progeny grown in Louisiana and North Dakota. In general, heritability estimates were quite comparable to those found by other researchers. Cunningham (21) found heritability estimates for specific gravity to vary from 21.0 to 64.0 per cent when based on the means of individual varieties grown in Wisconsin for two years. One might assume that if values for heritability estimates are over 50.0 per cent, progress for selection of specific gravity can be made in either Louisiana or North Dakota. This information alone is encouraging to the plant breeder, since it indicates selection efficiency and the possibility that exists within several different parental recombinations.

The significant negative correlation coefficient found between maturity and specific gravity of most all progeny lines grown in Louisiana was interesting. The effect of selection for one character on the expression of a second character is of interest for genetic improvement of all crops. This association between specific gravity and maturity might be utilized in a breeding program as an effective technique in selecting for high specific gravity varieties adapted to conditions in Louisiana. Data from this study indicated that this technique would not be applicable for progeny grown in North Dakota, as there was little or no correlation between specific gravity and maturity of clones tested at this location.

Low and variable correlation coefficients were found between specific gravity and vigor for progeny tested in both Louisiana and North Dakota. The only progeny showing association between these two characters was the progeny lines grown in Louisiana from the three Bounty crosses and Norland crossed with TL 1859. A significant negative correlation coefficient was found for these four progeny lines indicating that the least vigorous clones produced the highest specific gravity. Since at least one or more of the parents involved in these crosses expressed high vigor and late maturity, these parental characters certainly must have been contributing factors for the association of specific gravity and vigor. Apparently the highly vigorous, late-maturing clones could not manufacture and store carbohydrates as efficiently as the early-maturing, less vigorous clones in these four crosses.

Although maturity was positively correlated between progeny grown in Louisiana and North Dakota, data collected on plant maturity showed that clones matured earlier under the shorter days in Louisiana. These results are comparable to those found by Miller and McGoldrick (45). The overall progeny mean for clones grown in Louisiana was approximately .5 rating points earlier than similar clones grown in North Dakota. This would mean that for the same number of growing days clones grown in Louisiana matured approximately ten days earlier.

The segregation in progenies from all varieties used as parents showed that they were highly heterozygous for maturity. Several investigators have reported that potato varieties are heterozygous for maturity and that this character is controlled by many genes. Data from this study would be inclined to support such an hypothesis. When comparing the crosses of the combinations early x medium and late x late, an almost equal number of clones were represented in the early and medium maturity class; however, the early x medium crosses had a larger representation in the very early class and the late x late crosses were inclined to have more progeny in the very late class. Genetic influence for the early-maturing variety Norland was quite evident as both crosses involving this parent represented the highest number of clones in the very early and early classes. The findings were applicable to conditions in either Louisiana or North Dakota; however, environment was such in Louisiana that clones matured earlier.

Heritability estimates indicated that maturity was highly heritable and that selection could be made for this character regardless of whether the progenies were grown in Louisiana or North Dakota. Most progeny lines showed quite high heritability estimates.

When comparing the results from data collected in Louisiana and North Dakota, clones grown under the long days in North Dakota expressed more vigor and had more vegetative growth. Progeny tested in Louisiana and North Dakota showed a positive correlation coefficient for vigor; however, these correlations were slightly lower than that for maturity.

Like many other characters, the interplay of heredity and environment was also demonstrated by its effect on the expression of vigor. However, certain parental combinations had a marked influence on whether the clone had low or high vigor. Parental varieties having high vigor such as those represented in the crosses Bounty x 4524-16R and Bounty x ND 4524-7R produced the greatest number of progeny in the very vigorous classes. Segregation of progeny from all crosses indicated that parents were highly heterozygous for vigor. The poorest vigor was found in the two crosses having the parental variety Norland. In Louisiana, over 50.0 per cent of the progeny derived from Norland had very poor vigor. Poor vigor was also found for similar progeny tested in North Dakota.

The poor vigor of the variety Norland was also expressed in the heritability studies. This was particularly true for the cross involving Norland x Catoosa. The heritability value and the per cent selection advance would indicate that, if the potato breeder is attempting to maintain high vigor in his breeding stocks, he would avoid using parents like Norland that have poor combining ability for vigor.

The relatively high correlation coefficient for tuber shape when clones were grown in Louisiana and North Dakota indicated that this character was not influenced as much by environment as other characters studied. If a difference in the progeny mean for tuber shape was noted, expression seemed to be greater for a more round shaped tuber when grown in Louisiana. In many cases, it was quite difficult to determine the tuber shape category because many clones margined in the round, round-oblong or oblong-round class. Classification of oblong or long-shaped tubers was quite distinct within classes and classification was relatively easy. Very little difference in the number of clones represented in these classes was also noted when progeny was tested in either Louisiana or North Dakota. The high correlation coefficient indicated that selection for shape can be made in either the first or second clonal generation grown in either Louisiana or North Dakota.

Segregation of progeny for tuber shape was found for most parental recombinations indicating that parents were highly heterozygous for tuber shape. Early Gem, an oblong-long variety, and White Rose, a long variety, were the only parents to produce a high percentage of clones in the long class. When both of these parents were crossed with Katahdin, they produced over one-fourth of their progeny in the long-tuber class.

The two round varieties, La Chipper and Irish Cobbler, crossed with Katandin produced a high percentage of clones in the round class. Other recombinations showed a high degree of segregation; however, most all recombinations showed the largest representation of clones in the oblong class. Coefficient of variability, the ratio of standard deviation of the sample mean, was found to be high for most progeny.

For the most part, tubers grown in North Dakota had deeper eye depth than similar clones grown in Louisiana. Mean progeny ratings for eye depth in first and second clonal generations were positively correlated for all locations. The lowest correlation for all tests was found for first clonal generations grown in North Dakota and second clonal generations in Louisiana. However, correlation coefficient would indicate that selection could be made for eye depth regardless of whether progeny are grown in Louisiana or North Dakota and regardless of whether selection is made in the first or second clonal generation.

Although the pooled correlation coefficient for eye depth of second clonal generations grown in Louisiana and North Dakota were positively correlated, differences were noted between parental recombinations. For example, a much lower correlation coefficient was noted for the cross White Rose x Katahdin, and the three crosses having the parent variety Bounty. Of the four parents crossed with Katahdin, the progeny from La Chipper x Katahdin and Irish Cobbler x Katahdin showed the highest correlation coefficient. This would indicate that genetic influence for eye depth was more pronounced in the crosses involving the parents Irish Cobbler and La Chipper. Segregation in progenies from La Chipper and Irish Cobbler used as parents showed that these parents were highly heterozygous for the character eye depth. Other parental recombinations showed the amount of segregation one might expect when parents of different eye depth were used.

Estimates of heritability obtained for most all crosses indicated that eye depth was a heritable character and could be reliably selected. Although the cross Bounty x Viking was shown to produce a high per cent of progeny represented in the shallow-eye class, this cross did have the lowest heritability estimate and also the lowest per cent selection advance. Even though this is true, selection advance is still possible for this character. The correlation coefficients substantiated the heritability estimates showing that clones did not vary together and that a relatively high amount of environmental variance was present. A lower per cent selection advance would also be possible if the unit gain was small and the population mean was high. Per cent selection advance is a product of the selection differential and an estimate of heritability in the broad sense.

The positive correlation coefficient found between first clonal generation ratings for tuber appearance to ratings of the same clones from the second clonal generation grown in North Dakota and Louisiana the following year showed some relationship. However, of all the characters included in this study, tuber appearance expressed the lowest correlation between generations and locations. When comparing the data from progenies grown as first clonal generation in North Dakota to second clonal generation grown in Louisiana and North Dakota, a low level of association was found. Apparently tuber appearance is a character for which one cannot reliably select in the first clonal generation. It would seem necessary to consider the first clonal generation rating plus the second clonal generation rating to adequately select for this character.

There are many factors to consider when selecting for tuber appearance. First of all, tuber appearance is based on subjective rating and is much more exposed to human error; and second, several factors such as shape, size, and amount of external defects all contribute to its manifestation. No doubt the reason that the highest correlation was found for the second clonal generation grown in Louisiana and North Dakota was that many clones with poor appearance in the first clonal generation went through a process known as juvenility effect when they were grown as second clonal generation.

Estimates of heritability obtained for tuber appearance were quite variable and low among the different progeny lines. This was expected as the correlation coefficient for tuber appearance between second clonal generations grown in Louisiana and North Dakota was also low and varied. Expected selection advance was likewise low and variable between progeny lines. With some progeny lines there was only a 4.3 per cent selection advance from the second to the third clonal generation for tuber appearance. The per cent expected selection advance was determined by selecting the top 10.0 per cent of the clones within a progeny line having good tuber appearance in Louisiana and North Dakota.

Although heritability estimates for tuber appearance obtained for all three clonal tests indicated a wide range among progeny lines, the lowest heritability estimates were found between the first clonal generation in North Dakota and the second clonal generation in Louisiana.

When comparing data from the first clonal generation grown in North Dakota and the second clonal generation grown in either Louisiana or North Dakota, several progeny lines exhibited a zero heritability estimate. The heritability estimates indicated that selection for tuber appearance would be unreliable for certain crosses under consideration. The low heritability estimates for certain crosses showed that a greater percentage of the variance was due to environment and lesser percentage was genetically controlled. This analysis is certainly possible when one considers the factors associated with tuber appearance. Photoperiod, rainfall, temperature, soil texture, and soil-borne diseases all affect tuber appearance. The small number of widely-adapted, excellent-appearing varieties released in the past twenty years is further evidence that environment has a great effect on tuber appearance.

Other characters such as plant maturity, plant vigor, tuber eye depth, and tuber shape do not have as many interacting environmental factors affecting their phenotype. For example, a variety with good vigor at one location has relatively good vigor when grown under another set of environmental conditions. However, when one considers tuber appearance, such factors as finer soil texture, over-abundance of rainfall, and high temperatures all have the potential alone or together to cause serious external tuber defects which will lower the tuber appearance rating.

Segregation in progenies for tuber appearance was evident for all parental recombinations. Most clones were represented in the medium and good tuber appearance class. Inherent differences for tuber appearance were found for several parental recombinations. The crosses

La Chipper x Katahdin, Irish Cobbler x Katahdin, Bounty x ND 4524-16R, Bounty x ND 4524-7R, and Bounty x Viking expressed the highest level of combining ability for good tuber appearance.

In this study, the interaction of environment and phenotypic expression was found to be quite great for several characters. This is important as progeny tested in Louisiana and North Dakota were grown under extremely adverse environmental conditions. It was interesting to note that certain characters like specific gravity and tuber appearance were affected more than other characters by the forces of environment. It was also interesting to find that certain parental varieties like White Rose were found to have low heritability estimates for specific gravity and other characters. This would be relatively easy to understand as there never has been a good variety released that has White Rose in its pedigree. On the other hand, progeny from the parent variety Katahdin generally showed high heritability estimates for all characters. Katahdin is used extensively in most all breeding programs, and almost all of the new varieties released in the past few years can have its pedigree traced back to this variety.

Estimates of heritability for maturity, vigor, and eye depth showed that selection can be made quite efficiently in either Louisiana or North Dakota. Predicted selection advance also showed that progress can be made by selection providing certain parental recombinations are made. Estimates of heritability for specific gravity indicated that selection is more efficient if high specific gravity parents are used. Expected selection advance showed that if high specific gravity parents are used substantial gains can be made in specific gravity for clones grown in either Louisiana or North Dakota.

Several observations in this study illustrate the problems with which a potato breeder is confronted when he attempts to develop potato varieties adapted to such wide environmental conditions as those found in Louisiana and North Dakota. In this study, correlation coefficients and estimates of heritability varied for each character and for each parental recombination. Heritability estimates for each character either showed a relatively low or high variability between progeny lines. For example, a wide spread in magnitude of heritability for specific gravity of certain parental recombinations was noted. This could be expected as several investigators have reported that specific gravity is greatly affected by the forces of environment. However, the fact that certain parental recombinations reacted in a similar manner was encouraging.

Inferences made from heritability values determined for a character or cross other than the one being considered have been found to be unreliable. This was illustrated by the low and variable estimates of heritability found for the character tuber appearance. In some cases, the same parental recombination would show high heritability in one clonal test at a certain location, while in another test it would equal zero. As stated previously, this was not the case for specific gravity and other characters which showed relatively little difference in heritability between parental recombinations grown in different clonal tests. Mullins (47) also found low heritability for tuber appearance when he used second clonal generation progeny grown in North Dakota and Minnesota.

It is a common practice for most potato breeders to select for all characters in the first clonal generation. The fact that most all parents are highly heterozygous for all characters and that relatively large populations must be grown to properly select for a character, it is almost a necessity that a fairly high degree of selection has to be made in the first clonal generation. This study showed that when proper parental recombinations are made, selection is fairly efficient in the first clonal generation for all characters except tuber appearance. Even in some cases selection for tuber appearance is possible in the first clonal generation, but one should realize its limited effectiveness.

The effect of selecting for one character on the basis of expression of another character has limited value for certain characters and certain sets of environmental conditions. The relatively high negative correlation between maturity and specific gravity for progeny grown in Louisiana has been discussed. However, in this study the two most highly correlated characters were vigor and maturity. The magnitude was such for these two characters that selection on the basis of one character could be expected to be concurrent with selection for the other. This was true for progeny grown in either Louisiana or North Dakota.

Data from this study indicated that progress can be made in developing wider adapted potato varieties if proper parental recombinations are made. If desirable recombinations are made in an asexual crop such as potatoes, the breeder can take advantage of outstanding individuals occurring at any stage in a breeding program. This has been illustrated with several asexually propagated crops (29; 30; 36).

SUMMARY

Studies were made to determine the effect of environment on the genetic behavior of certain quantitative characters found in the Irish potato, Solanum tuberosum. Special emphasis was placed on specific gravity. Concurrent studies were also made on the phenotypic variability of plant maturity, vigor, tuber shape, tuber eye depth, and tuber appearance.

Ten progeny lines representing several hundred clones were grown at Baton Rouge, Louisiana, and Grand Forks, North Dakota. Progeny lines representing first clonal generations were grown in the North. Second clonal generations were grown both in the North and South. Twelve parents, which represented a wide range in horticultural characters, were used to develop progeny lines.

The segregation in progenies from all the varieties used as parents showed they were heterozygous for all characters. Data from specific gravity studies showed that progenies from crosses between low x medium and low x high specific gravity parents generally produced the highest degree of segregation. The crosses between high specific gravity parents gave the highest mean specific gravity for its progeny. Several of the clones from high specific gravity parents were as high or higher in specific gravity than either parent.

Specific gravity of tubers from progenies of second clonal generations were found to be high in the North and low in the South. Tubers from progenies of first clonal generations grown in the North were intermediate in specific gravity.

The pooled correlation coefficient for all characters from

progenies grown as second clonal generations in the North and South showed some degree of linear relationship. The lowest association was found for specific gravity and tuber appearance. The highest association was found for tuber shape, indicating that most tubers retained their shape regardless of whether they were grown in the North or South. In comparing progenies from the first clonal generation to those of the second clonal generation, the lowest association was found for tuber appearance. Specific gravity and eye depth showed the next lowest association.

Correlation coefficients showed that differences in the magnitude of the association for certain characters were affected by parents used in developing the progeny lines. A high correlation coefficient was found for progeny lines from crosses involving high specific gravity parents. The correlation coefficient for plant vigor from progenies grown in the North and South generally showed the highest relationship for progenies resulting from vigorous parents. Parents differing in eye depth showed a relatively high relationship for progenies from deep-eyed parents. Tuber appearance showed low and variable association for progenies from different parental combinations. For late plant maturity, the lowest association for clones grown in the North and South was found when two early-maturing parent varieties were crossed.

The effect of selecting for one character on the expression of a second character was exhibited for plant maturity and vigor. The latest maturing clones exhibited the highest vigor when grown in the North and South. Specific gravity and maturity were negatively correlated for clones grown in the South, indicating that the earliest maturing clones produced the highest specific gravity. No association was found between specific gravity and maturity when clones were grown in the North.

In the South the association between plant vigor and specific gravity was effective only from progeny resulting from high vigor parents. The negative correlation for progeny with high vigor parents indicated that the least vigorous clones produced the highest specific gravity. Little or no association was found for plant vigor and specific gravity for progeny tested in the North. Correlation coefficients computed between the other characters included in this study indicated that, in general, the factors were independent and therefore could not be utilized for predictive purposes.

Estimates of heritability of several characters were computed using data from progenies representing first and second clonal generations grown in the North and South. For progenies from second clonal generations, estimates for heritability of specific gravity and tuber appearance were lower than the heritability estimates of plant maturity, vigor, and tuber eye depth. Estimates of heritability for tuber appearance were low and variable when analyses were made between first clonal generations grown in the North and second clonal generations grown in the North and South.

Estimates of heritability and expected selection advance varied for each character and for each progeny line. For specific gravity, the progenies resulting from high x high specific gravity parents produced the highest per cent selection advance. When considering data from all progeny lines, the per cent selection advance was found to be the highest for plant maturity and vigor and lowest for tuber eye depth, tuber appearance, and specific gravity. The wide range in per cent selection advance for each character suggested that there were differences among progeny lines in superiority of the specific factor considered.

This study showed that although the forces of environment affected the genetic behavior of all characters, selection for several characters in the first or second clonal generation could be made quite efficiently in the North or South. Under environmental conditions found in Louisiana and North Dakota, selection could be made efficiently for plant maturity, vigor, tuber shape, and eye depth. A lesser degree of selection efficiency was found for specific gravity and tuber appearance. Northern environmental conditions produced the highest specific gravity, but if proper parental combinations were made, which would result in a higher gene concentration, selection of clones relatively high in specific gravity could be made at both locations. Tuber appearance seemed to be the character most affected by environment.

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APPENDIX

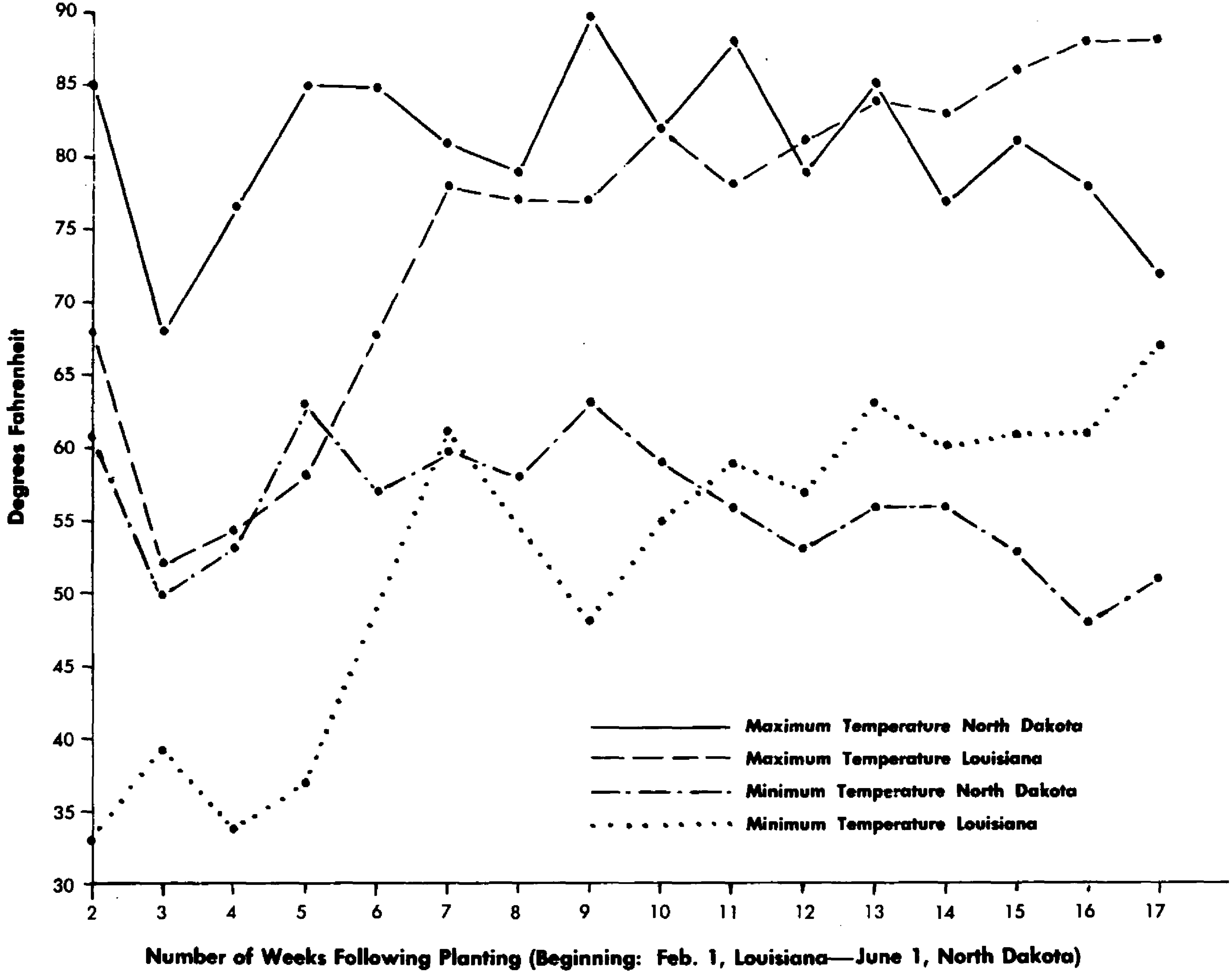

Fig. 1. Maximum and Minimum Temperatures During 1963 Growing Season in Louisiana and North Dakota

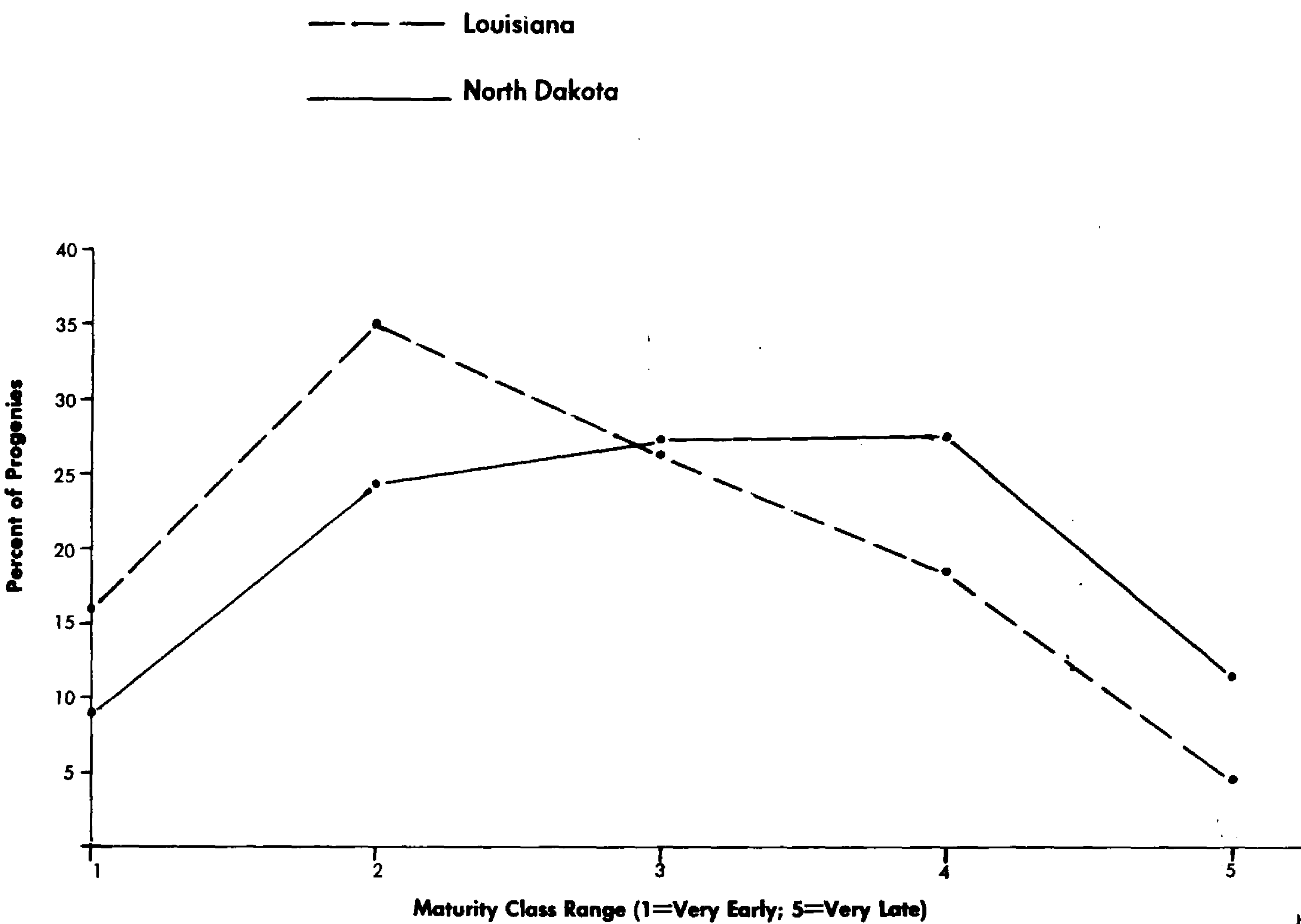

Fig. 2. Effect of Location on Plant Maturity of Progeny Lines

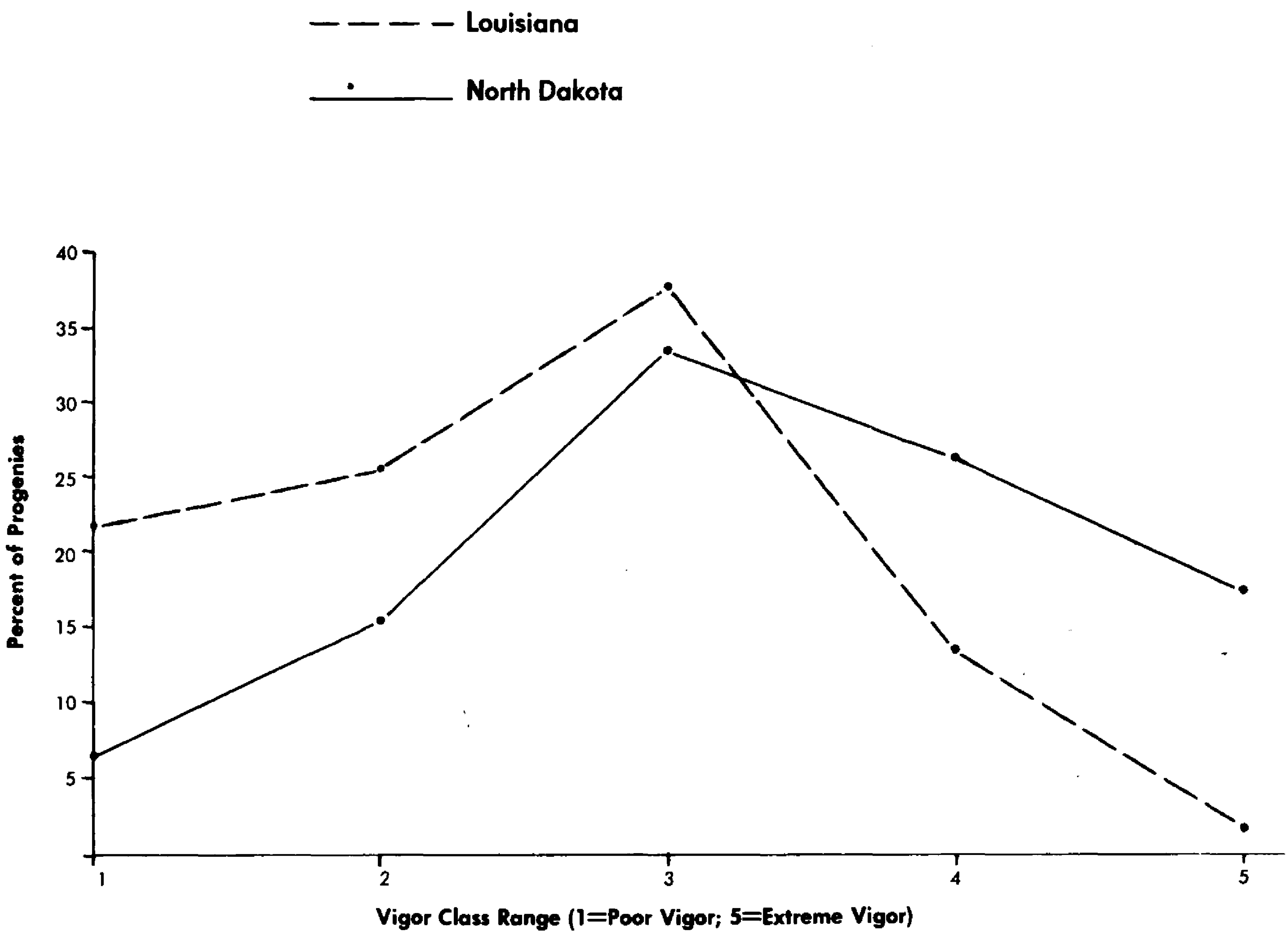

Fig. 3. Effect of Location on Vigor of Progeny Lines

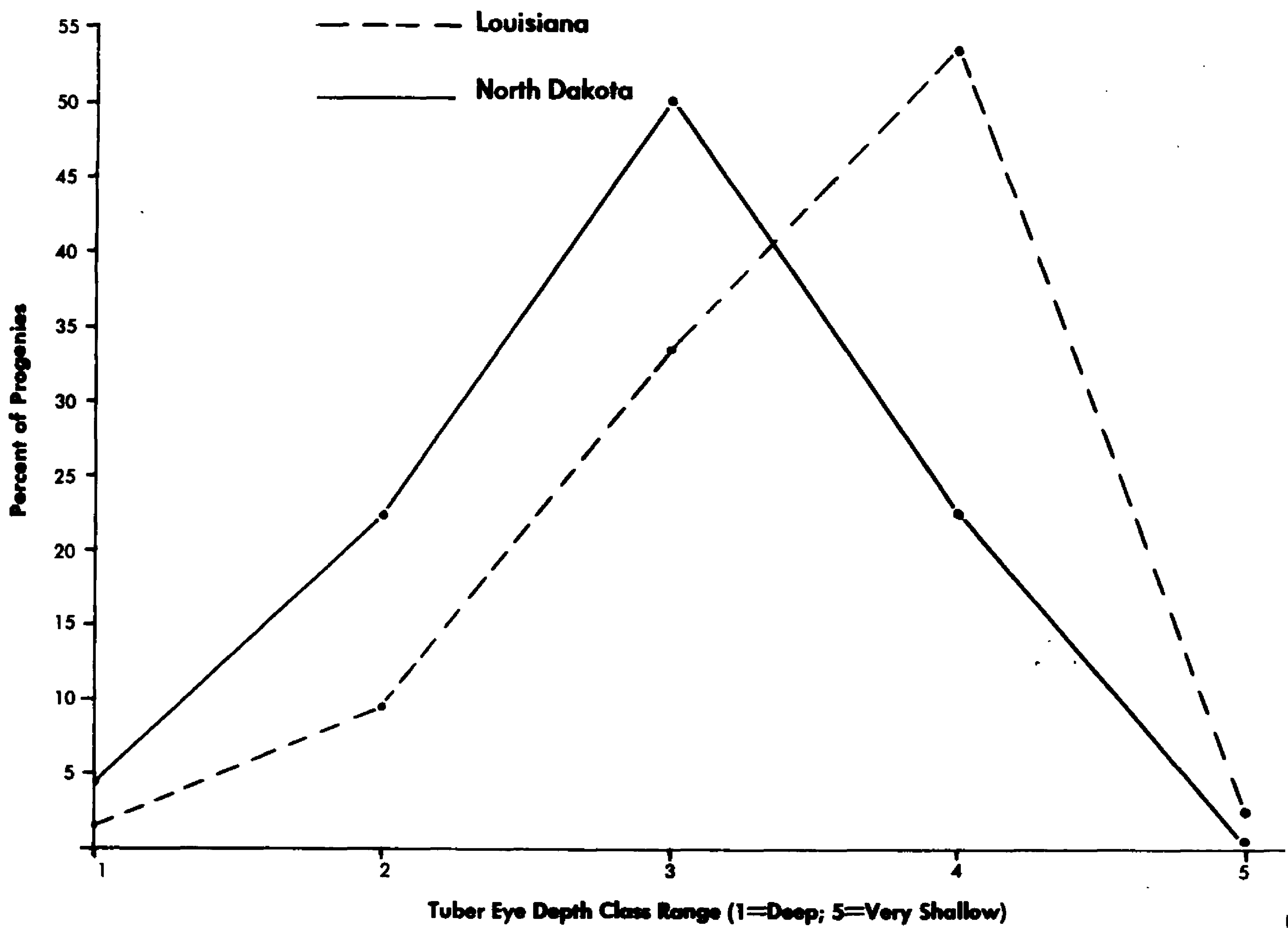

Fig. 4. Effect of Location on Tuber Eye Depth of Progeny Lines

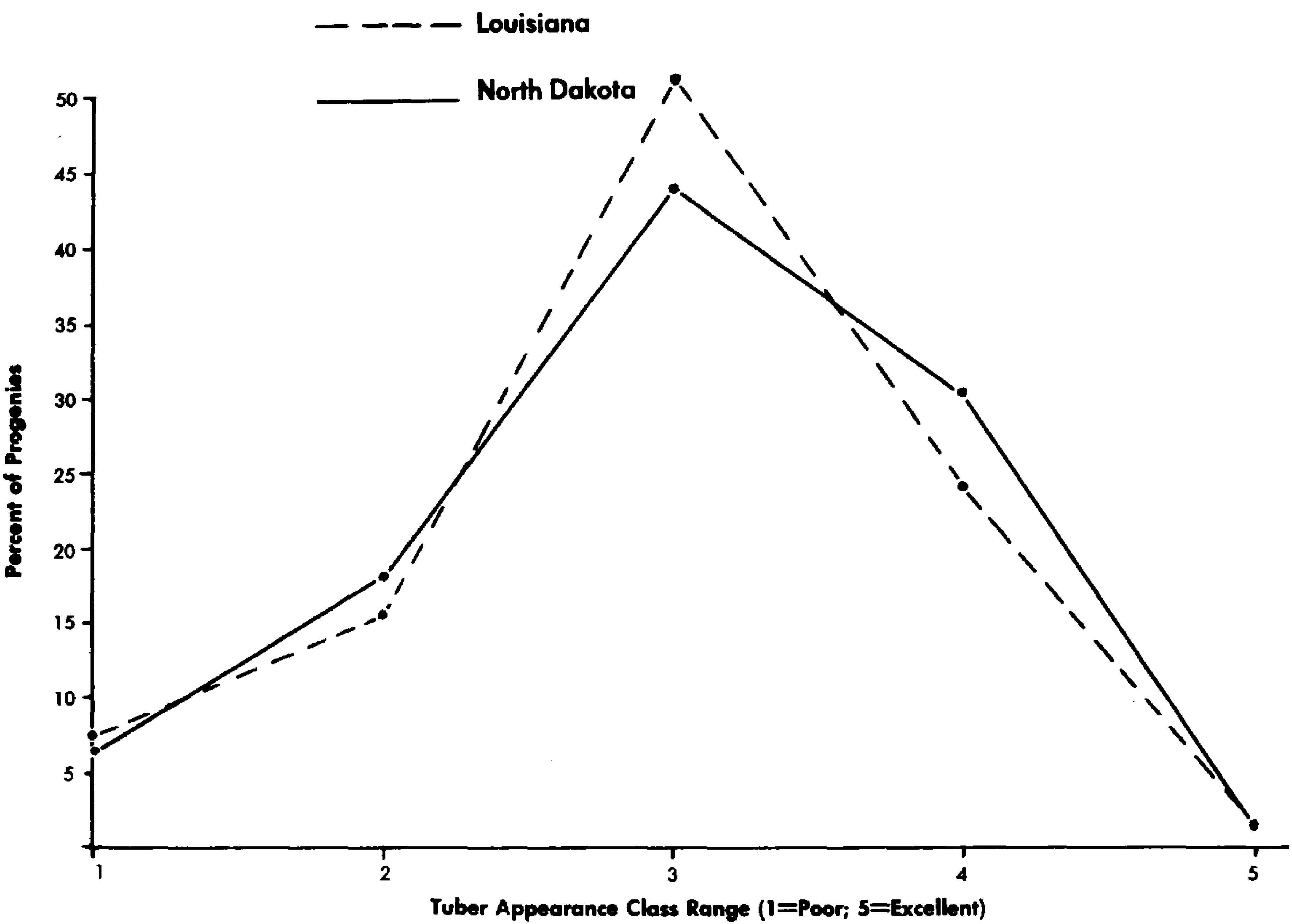

Fig. 5. Effect of Location on Tuber Appearance of Progeny Lines

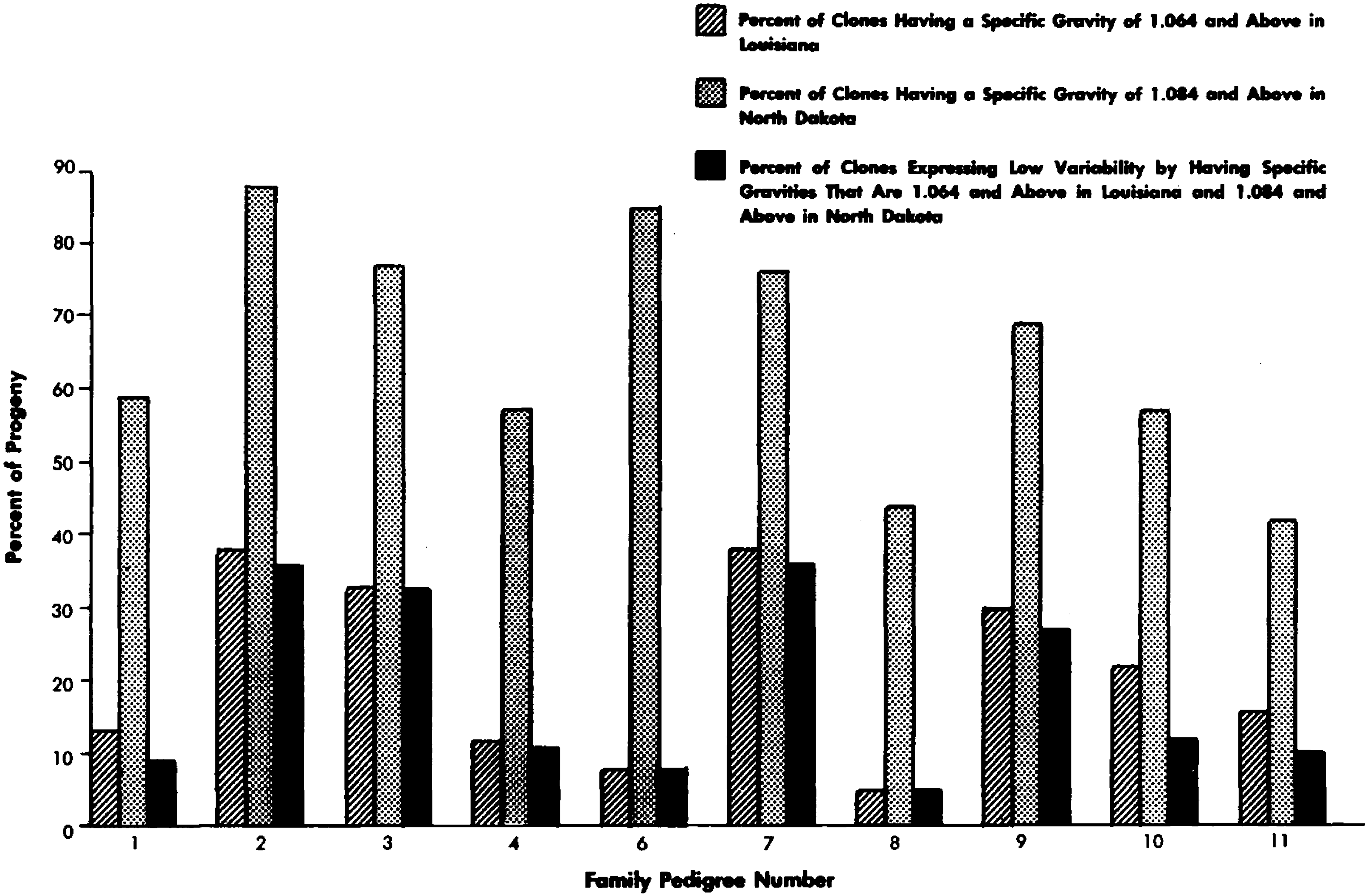

Fig. 6. Effect of Location on Selecting for High Specific Gravity

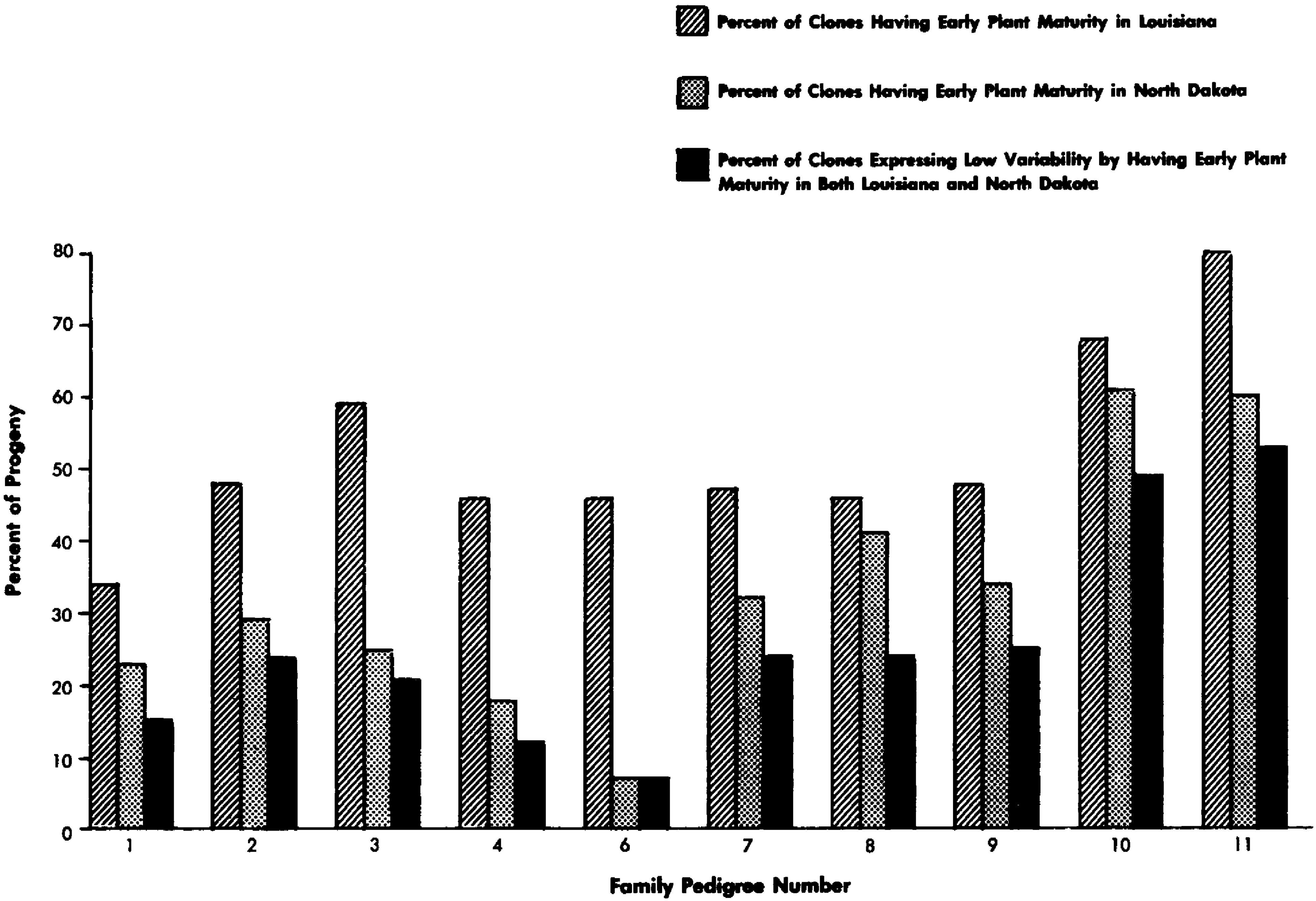

Fig. 7. Effect of Location on Selecting for Early Plant Maturity.

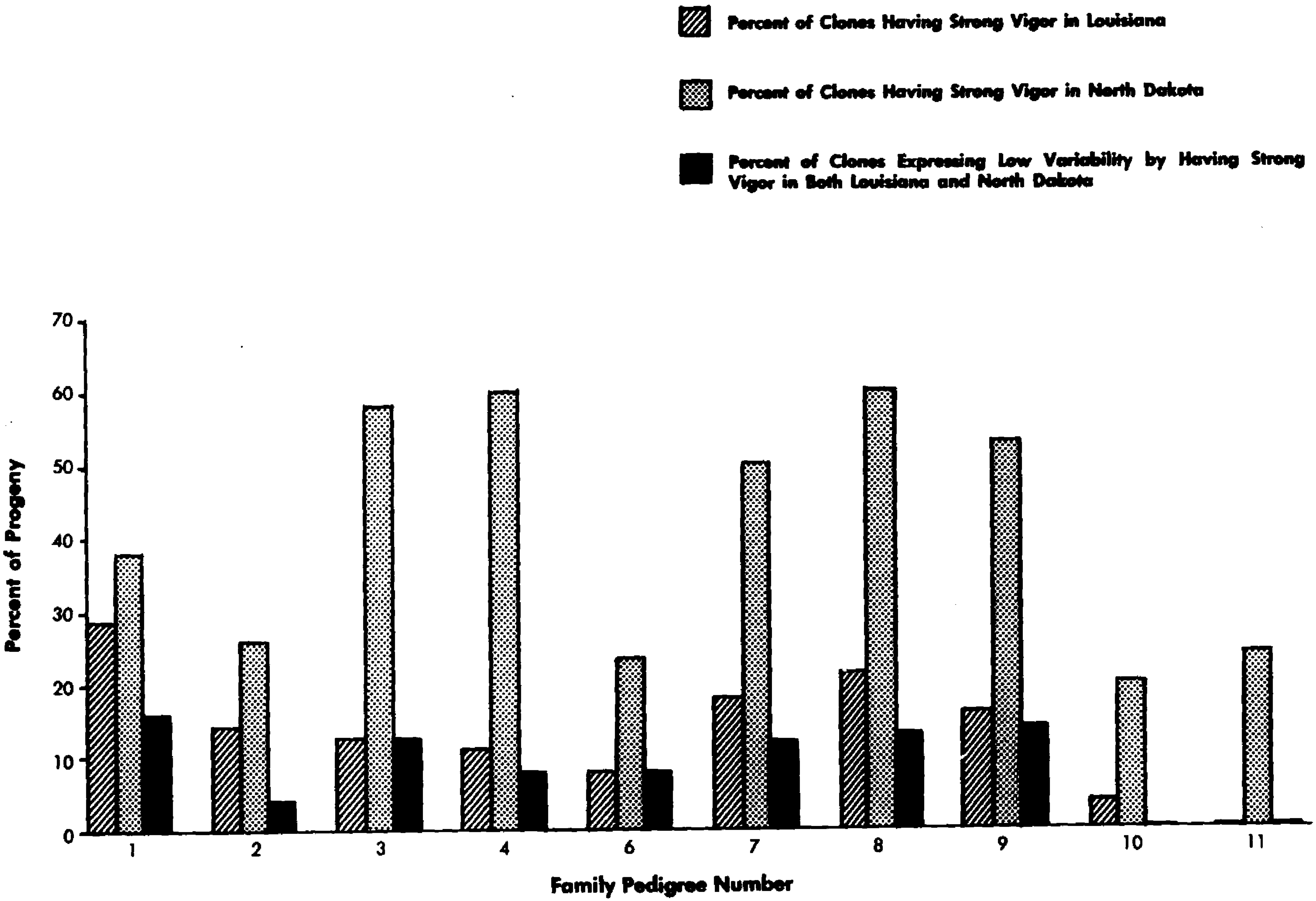

Fig. 8. Effect of Location on Selection for Strong Vigor

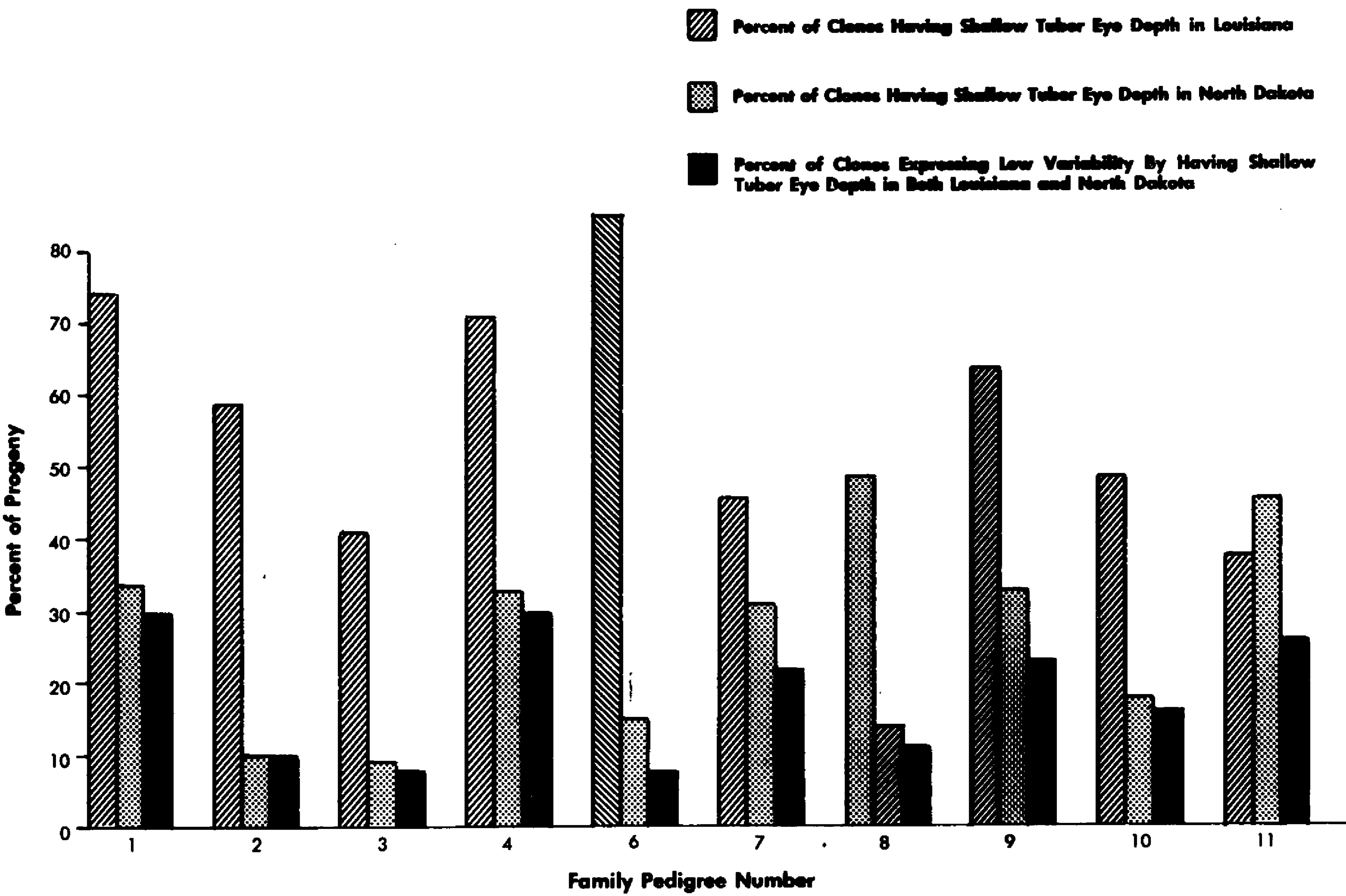

Fig. 9. Effect of Location on Selecting for Shallow Tuber Eye Depth

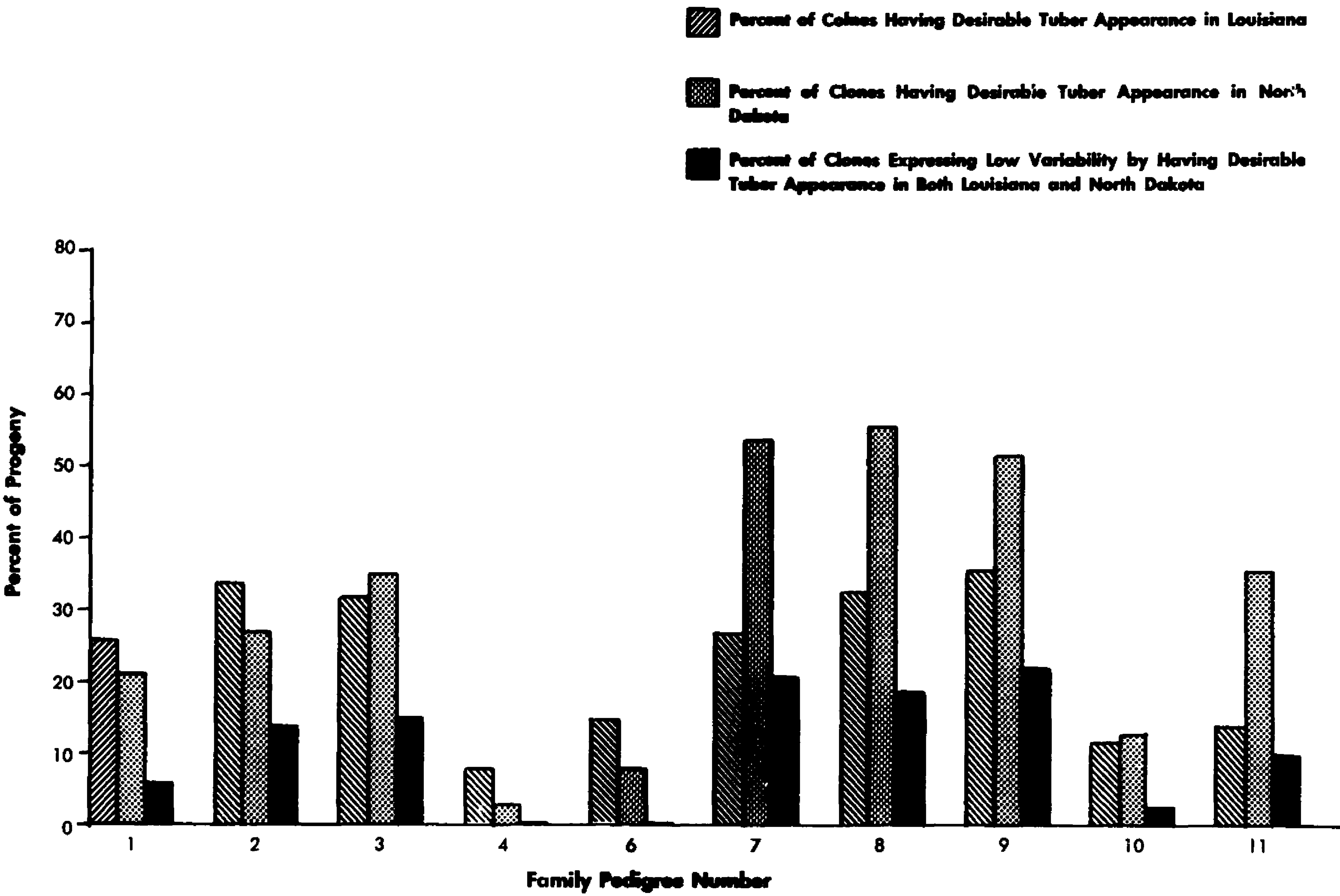

Fig. 10. Effect of Location on Selecting for Desirable Tuber Appearance

AUTOBIOGRAPHY

Robert H. Johansen was born at Grafton, North Dakota, July 25, 1922. His early childhood was spent on his father's farm near Edinburg, North Dakota. In 1940 he graduated from high school at Park River, North Dakota, and in 1941 he enrolled at the North Dakota State University. His college career was interrupted in 1944 when he enlisted in the United States Navy. He served with the Navy in both the Pacific and Atlantic theaters of war until he was honorably discharged in 1946. In 1947 he again enrolled at the North Dakota State University and received his Bachelor of Science degree in 1949. In 1950 he was employed by the Horticulture Department at North Dakota State University to work on potato breeding. In 1956 he received his Master of Science degree in Horticulture and Botany at North Dakota State University. In 1961 he enrolled at Louisiana State University and is now a candidate for a Doctor of Philosophy degree in Horticulture and Agronomy. His present position is Associate Professor of Horticulture in charge of potato breeding at North Dakota State University.

EXAMINATION AND THESIS REPORT

Candidate: Robert H. Johansen

Major Field: Horticulture/Agronomy

Title of Thesis: The Effect of Environment on the Genetic Behavior of Irish Potato Progenies.

Approved:

Julian C. Miller

Major Professor and Chairman

Max Goodrich

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Date of Examination:

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